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REPRODUCTIVE ECOLOGY OF AMERICAN OYSTERCATCHERS IN THE CAPE ROMAIN REGION OF SOUTH CAROLINA: IMPLICATIONS FOR CONSERVATION

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REPRODUCTIVE ECOLOGY OF AMERICAN OYSTERCATCHERS IN THE CAPE ROMAIN REGION OF SOUTH CAROLINA: IMPLICATIONS FOR CONSERVATION

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ABSTRACT

The Cape Romain Region (CRR) is located along the coast of South Carolina and supports over half of the breeding pairs (approximately 200 pairs) of American Oystercatchers (*Haematopus palliatus)* in the state. Research has shown that oystercatcher productivity in this area is low due to predation and over-wash from high tides and boat wakes. I assessed the feasibility of using headstarting as a means of reducing nest loss in an attempt to enhance reproductive success during the 2010 and 2011 breeding seasons. Apparent nest success of headstarted nests (52%) was higher than control nests (11%) along two study areas within the CRR. However, apparent brood success was higher for control nests (90%) compared to headstarted nests (27%). Although headstarting did improve nest success during incubation, it did not appear to ultimately enhance productivity within this region because of high rates of chick loss.

In addition to assessing the feasibility of headstarting, I also examined attributes of behavior and attendance rates of oystercatcher breeding pairs on nesting territories in two study areas of the Cape Romain Region. I recorded the percentage of time breeding pairs were present on nesting territories and the behaviors exhibited while present during low-tide foraging periods during incubation and chick rearing. I found no significant differences in the rate of attendance or each behavior between breeding pairs with assigned headstart or control nests for incubation and chick rearing. Attendance of breeding pairs was found to be significantly related to the nest success of control nests but was not found to be related to the brood success of chicks. Behavior of breeding pairs was often found to be significantly related to site during incubation and chick age during chick rearing.

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INTRODUCTION

The reproductive success of shorebirds is limited by many factors including inclement weather and flooding, prey availability, food availability, habitat disturbance, inter- and intra-specific competition, and predation (McGowan and Simons 2006; Sabine et al. 2006; Smith et al. 2007; Thibault 2008). These ecological stressors may vary among locations and years, and act alone or interact with other anthropogenic drivers such as coastal development and human population growth. These limiting factors on reproductive success can drive fluctuations in the abundance and geographical distribution of birds (Gill 1995). Decreases in abundances and shifts in distributions are a concern for shorebirds worldwide (Brown et al. 2001). By identifying factors that contribute to decreased reproductive success of shorebirds we can better develop and implement effective management strategies for species of conservation concern.

A shorebird that may be vulnerable to some of these extrinsic factors along the southeastern coast of the U.S. is the American Oystercatcher (*Haematopus palliatus*). This coastal nesting species experiences highly variable reproductive success among years and among locations and is intolerant to high levels of disturbance (Sabine et al. 2006). American Oystercatchers are long-lived and demonstrate variable breeding success among years (Nol and Humphrey 1994). The American Oystercatcher is considered a species of high concern by the U.S. Shorebird Conservation Plan due to its low population size of *ca.* 10,000 and of these only 3,000 individuals are likely breeding adults (Brown et al. 2001). While there is evidence of range expansion in the northeastern U.S., American Oystercatcher population estimates indicate a decline in the mid-Atlantic (Mawhinney et al. 1999; Davis et al. 2001).

The American Oystercatcher breeds along the Atlantic Coast from Massachusetts to Florida (Nol and Humphrey 1994). They nest on barrier beach islands, salt marshes, dredge spoils and shell mounds (Lauro and Burger 1989; Toland 1992; Wilke et al. 2007). Oystercatchers scrape shallow depressions in the substrate and normally lay 2-3 eggs. Both adults incubate the clutch for approximately 27 days and provision chicks long after they fledge (~35 days). South Carolina supports over 400 pairs of breeding oystercatchers, the majority of which nest on washed oyster shell mounds within the Cape Romain Region of the state (Sanders et al. 2008).

The purpose of this study was to investigate the reproductive ecology of American Oystercatchers in a core portion of their breeding range and assess conservation strategies that may enhance productivity. Results from surveys conducted by SC DNR and from previous research efforts suggest that reproductive success of this species within the Cape Romain Region may vary spatially and temporally within and among habitats (Sanders et al. 2008; Thibault 2008). For example, Thibault (2008) found that approximately 85% percent of American Oystercatcher nests monitored within the Cape Romain region of South Carolina during the 2006 and 2007 breeding season failed to hatch primarily due to flooding (i.e., high tides or overwash of nests from waves) and predation of nests. Results also suggest that overwash and predation may also contribute to chick mortality. Examining potential conservation strategies that may improve the reproductive success of oystercatchers within this area may be necessary to aid in maintaining sustainable populations.

Chapter two of this thesis, "Feasibility of Headstarting as a Conservation Tool for American Oystercatchers within the Cape Romain Region of South Carolina", examines headstarting (i.e., collecting designated clutches during incubation, incubating clutch in a controlled setting, and returning chicks to nest immediately after hatch) as a means of enhancing productivity of American Oystercatchers nesting in two locations within the Cape Romain Region. I assigned breeding pairs as headstart or control based on the order in which nests were found then measured the nest success and brood success of all nests. The hatch success of eggs in the incubator was assessed and I attempted to identify the causes and timing of nest failure and chick loss in the field for both nest types during the 2010 and 2011 breeding seasons.

Chapter three of this thesis, “Attendance and Behavior of American Oystercatcher Parents During the Breeding Season in the Cape Romain Region of South Carolina”, examines the behavior and attendance rates of oystercatcher pairs with active nests during the breeding season. I conducted surveys on breeding pairs during incubation and chick rearing for the 2010 and 2011 breeding season. During these surveys, I recorded the percentage of time breeding pairs of oystercatchers were present on their nesting territory, as well as the behaviors adults exhibited while in attendance on nesting territories in two different locations during the foraging period.

Understanding the reproductive ecology of the American Oystercatcher is an important step in managing populations within the Cape Romain Region. This involves knowledge of behavioral differences between sites and years as well as the feasibility of using a conservation tool, such as headstarting, to enhance productivity.

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CHAPTER II

FEASABILITY OF HEADSTARTING AS A CONSERVATION TOOL FOR AMERICAN OYSTERCATERS WITHIN THE CAPE ROMAIN REGION OF SOUTH CAROLINA

INTRODUCTION

The American Oystercatcher is considered a species of high concern by the U.S. Shorebird Conservation Plan because of the low and declining population size along the Atlantic coast (Brown et al. 2001). Studies estimating American Oystercatcher populations have indicated there is a decline in states south of Virginia (Mawhinney et al. 1999; Davis et al. 2001). Threats from coastal development, recreational disturbance, increased predation rates associated with human activity, and climate change are concerns for this long-lived species (Davis et al. 2001, McGowan 2004, Thibault 2008).

South Carolina supports the second largest number of American Oystercatcher breeding pairs (*ca*. 400 pairs) within any state on the Atlantic coast and over half (*ca*. 230 pairs) of these nest within the Cape Romain Region (Sanders et al. 2008). The Cape Romain Region (CRR) is located north of Charleston and is adjacent to the Cape Romain National Wildlife Refuge (CRNWR). The Region also serves as an important site for the population during the non-breeding season with *ca*.1900 wintering oystercatchers (Sanders et al. 2004). This area provides an abundance of suitable nesting and foraging habitat for this species. Oystercatchers in this Region nest primarily on mounds of washed shells along waterways and in bays as historical beach nesting habitat has been lost to coastal development and current beach habitat experiences disturbance by humans (Sanders et al. 2008). Results from previous research in this area suggest that productivity appears to be low and variable between sites and years and multiple factors may contribute to variable and low productivity (Thibault 2008). For example, wakes from boat traffic and storm overwash contribute to nest failure but it is not clear to what extent, if any, microtopography (e.g., elevation, slope; Hazlitt 2001) of nest sites may affect reproductive success. Predation of nests and chicks by a variety of predators also occurs in American Oystercatchers in the CRR (Thibault 2008) as well as in oystercatcher species worldwide (Hockey 1996) but the extent of predation may differ among habitat types, years, or stages of the breeding cycle. Other factors such as human disturbance and habitat alteration may also affect reproductive success of oystercatchers in Cape Romain (Thibault 2008).

Given the evidence of low and/or variable annual productivity and declining populations in the mid- and south Atlantic states, methods to enhance reproductive success of oystercatchers in this region are currently being considered. One suggestion has been to "headstart" nests. A headstart program entails the following steps: (1) collecting real eggs from the nest during incubation, (2) replacing collected eggs with artificial eggs painted to resemble oystercatcher eggs that are secured to the scrape with an anchor, (3) incubating real eggs in an incubator in a controlled setting and (4) pulling artificial eggs from the scrape and releasing chicks back into the nest immediately after hatch. If productivity is lost primarily during the incubation stage due to factors such as flooding or predation as appear to be common for oystercatchers, then headstarting nests may enhance oystercatcher productivity by improving nest success. In contrast, if productivity is primarily or additionally lost during chick rearing, then headstarting may not provide a means to enhance reproductive success for this species.

The goal of this study was to assess the feasibility of using a headstarting program to enhance reproductive success of American Oystercatchers in a core portion of their breeding range. I used a control-impact approach to assign nests as either control or headstart nests and then measured the success of these nests and determined likely causes of failure when it did occur. I also measured the success of hatching in the incubator, and the success of parents accepting headstarted chicks. These data therefore provide an initial assessment of the effectiveness of a headstarting program for producing chicks and identify potential factors that contribute to reproductive failure.

METHODS

Study Area

The Cape Romain Region (Figure 2.1) is comprised of barrier islands, shallow bays, tidal creeks, salt marsh (dominated by *Spartina alternaflora)*, mudflats and oyster (*Crassostrea virginica*) reefs. The Cape Romain Region (CRR) encompasses the Cape Romain National Wildlife Refuge (CRNWR) and is the central location for numerous research projects on shorebirds and nearshore seabirds (Ferguson 2006; Hand 2008; Jodice et al. 2007; Sanders et al. 2008; Thibault 2008; Brooks 2011). Elevated shell mounds of oyster and clam (*Mercenaria sp*.) shells formed by wind and wave energy along sections of bays, estuarine islands and waterways provide nesting habitat for approximately half of nesting oystercatcher pairs in South Carolina (Sanders et al. 2008). I monitored oystercatcher nests on shell mounds in two study areas during the breeding seasons of 2010 and 2011: along the Atlantic Intracoastal Waterway (AICW) adjacent to the CRNWR and in the southwestern section of Bulls Bay within CRNWR (Figure 2.1). The AICW is a navigable waterway that has seasonal migrations of large boats that can create substantial wakes which wash over shell mounds. In contrast, the southwest section of Bulls Bay does not receive much human recreational disturbance and is shallow and surrounded by *Spartina* salt marsh.

Nest Monitoring

Nest searches began in late March and continued through the end of July in 2010 and 2011. Shell rakes along the AICW, from marker 67 to 97 (*ca.* 12.6 km), and all shell rakes in the southwest section of Bulls Bay (Venning Creek to Bulls Island Creek) were searched approximately every three days until 1 July each year (nest initiation was not documented any later than mid- June). Oystercatchers are territorial during the breeding season and are very conspicuous and vocal on their territories when protecting a nest. Therefore, I was confident that I located nests for every active pair within the study area on days where nest searching occurred. However, it is possible that nests may have been initiated and lost between search days. I assumed the same pairs were making additional nesting attempts when re-nesting occurred on the same shell mound because American Oystercatchers are typically monogamous and show strong nest site fidelity (Nol 1989; Nol and Humphrey 1994). Furthermore, the majority of nesting pairs (75% in 2010, 68% in 2011) in this study had at least one banded adult identifiable by unique color combinations and within each breeding season, all pairs that renested remained within the same nesting territory. Once a nest was located, a 12 cm nail with an identification number was anchored into the shell mound about 1m from the nest as a marker. The location was recorded (± 3 m) using a handheld GPS, the number of eggs present in the nest was recorded, and the band combinations of any adults observed on the nesting territory also were recorded. To assess any occurrence of overwash or localized flooding, “overwash cups” were placed horizontal to and parallel with the nest scrape. I used 350 ml plastic cups that had holes near the top of the cup and a lid. Cups were glued to a wooden base with a large nail that was then secured in the shell substrate. The holes along the sides of the overwash cups allowed collection of salt water from overwash into the cup while the lids secured to the top prohibited rainfall from filling the cup.

Each discovered nest was classified as either a headstart nest or a control nest. I classified nests in the order in which they were found within each study area, alternating between headstart and control assignments. Once a nest was found and assigned as headstart or control, any renest attempts made by the pair on that site remained the original classification. For headstart nests I collected all but one egg from the clutch (hereafter referred to as 'original eggs'), with the exception of one egg clutches for which we collected the egg and left no original eggs in the scrape (17% of all clutches were one egg clutches, n=14). These nests were left out of the analysis of the survival of original eggs but were included in analysis of all headstart nests. The single egg that remained in the nest for headstart clutches greater than 1 egg served as an indicator of potential nest fate (e.g. I was able to use that egg to determine possible causes of nest failure such as predation or abandonment). I replaced the collected eggs in the nest with wooden artificial eggs that were painted to resemble oystercatcher eggs. Artificial eggs were deployed to encourage parents to continue to incubate so the nest would remain active. Artificial eggs were initially attached by string to a large nail that was secured into the scrape. However, this large nail was replaced with an 18" rebar anchor during 2010 after predators had pulled up artificial eggs and adults subsequently abandoned nests.

Eggs were collected from nests immediately if the clutch was complete and being incubated upon discovery (n=38) or, if the clutch was not complete and being incubated upon discovery, as soon as the clutch was complete (i.e., within 5 days after the first egg was laid; n=32). Occasionally, nests failed before I was able to collect the eggs from a complete clutch. This happened with 17% (n=14) of the assigned headstart nests. These nests were included in subsequent analyses of survival of real eggs that were left in the scrape but removed from subsequent analyses of survival for all assigned headstart nests with dummy eggs.

I labeled each collected egg with a nontoxic pen to identify its nest origin, transported the eggs to a facility located in CRNWR (maximum distance from any nest approximately 9 km), and placed the eggs in a cabinet-style incubator (Brinsea Ova-Easy 190). Eggs in the incubator were measured for length (L), breadth (B) and weight. Egg volume (cm^3) for collected eggs was calculated as Volume= 0.51 * LB^2 (Hoyt 1979). Eggs were monitored regularly for signs of hatching. Once chicks began to hatch, they were placed into a hatching tray until hatched and then returned to the original nest as soon as possible but always within 24 hours of hatching. After chicks were placed in the nest scrape, we observed nests to verify that adults accepted and brooded the returned chick. If artificial eggs were lost, washed away, or buried, or if adults discontinued incubation before the collected eggs hatched, chicks were fostered into another headstart nest with a similar estimated hatch date.

Active headstart nests in Southwest Bulls Bay and along the AICW were checked on average every three days (2.97 ± 1.41) until chicks were returned to the nest or the nest failed. During each nest check, I recorded the date, time, number of eggs (real and artificial), tide phase, and number of adults present. If no eggs (original or artificial) were observed in the scrape or parents appeared to have abandoned the nest, the territory was searched for any evidence that could assist in the determination of causes of nest failure (e.g., signs of flooding, predation, disturbance). Assigned headstart nests that failed before collection (i.e., eggs missing from scrape before clutch was complete and eggs could be collected for artificial incubation) were accounted for in the fate of headstart nests. Causes of nest failure for headstart nests with artificial eggs (i.e., parental abandonment) were classified as predation (signs of predation at the nest coincident with nest abandonment, e.g. teeth marks on artificial eggs or artificial eggs removed from scrape), overwash (overwash cup contained salt water, overwash cup dislodged from shell rake, recently deposited rack observed near/on nest or fake eggs buried under shells; any or all coincident with parental abandonment of artificial eggs), abandoned (adults continued to incubate artificial eggs after loss of real egg but adults not observed incubating for at least three visits, or new scrape discovered later in the incubation cycle but no signs of predation or overwash observed), undetermined (adults not observed incubating after loss of real egg and cause of loss of real egg unknown) and other (one event, adult in breeding pair was killed by predator, likely a peregrine falcon based on evidence from remains). For both sites and years, I report the hatching success of eggs in the incubator (percent of all eggs collected that hatch in the incubator and the percent of clutches that hatch ≥1 egg), the number of eggs left in a scrape that hatched, and the percent of pairs that continued to incubate nests until chicks could be returned (nest survival).

Active control nests in Southwest Bulls Bay and along the AICW were checked on average every three days (3.04 ± 1.07) until the nest hatched or failed. During each nest check, I recorded the date, time, number of eggs, tide phase, and number of adults present. Cameras were deployed for control nests found in Bulls Bay in 2011 from 21 April to 22 June to further assist with classification of nest loss and to identify potential nest predators (Sabine 2005; Thibault 2008; Brooks 2011). The system was revised to consisted of a SVAT mini digital video recorder (DVR) connected to a 7.6 cm waterproof infrared camera, powered by two 12-volt deep-cycle marine batteries which ran on parallel (Figure 2.2). The video camera was placed through a small hole cut in a 5-gallon plastic bucket that was lined with foam and was connected to the DVR with the use of a power inverter and AC to DC power adapter. All of the equipment was housed in the 5-gallon bucket with a watertight Gamma Seal^{TM} lid. The DVR was set to 352 X 240 resolution at 4 frames per second and used 8GB SD cards. The video camera was placed approximately 3m from nests. Batteries were replaced every visit and SD cards were changed weekly.

As with headstart nests, when a control nest failed the territory was searched for any evidence that could assist in the determination of causes of nest failure. Causes of nest failure in control nests were classified as predation (scat, eggshells or tracks observed near nest or depredation event observed on video), overwash (overwash cup contained salt water, overwash cup dislodged from shell rake, recently deposited rack observed near/on nest; any or all coincident), abandoned (adults not observed incubating eggs for three visits and egg feels hot/cold or new nest discovered) and undetermined (no signs of depredation or overwash).

I chose ‘nest success’ as the term for any nest that survives to hatch because of the confusion with headstart eggs hatching in the field or in the incubator. Nest success of control nests was defined as $\geq$ 1 egg in a clutch hatching. Hatch success was used to refer to collected headstart eggs in the incubator only. Because headstart nests have a greater chance of hatching with eggs in the incubator but adults may not remain at the nest to incubate artificial eggs, I defined nest success for headstart nests as either (a) parents continuing to incubate eggs (original or artificial) until the hatch date with at least one chick being successfully returned to the nest, and/or (b) parents successfully hatching the real egg that remained in the nest scrape.

Chick Survival

Oystercatcher chicks camouflage well on nesting territories and are mobile within a day after hatch. Therefore, I used radio telemetry to locate headstart chicks and more accurately determine timing and causes of chick loss in Southwest Bulls Bay and along the AICW. I used surgical glue to attach 1.3g transmitters (Advanced Telemetry Systems, Isanti, MN) to the scapular region of newly hatched headstart chicks before they were returned to the nest. Headstart chicks were returned to their original nest or placed in a suitable foster nest with their eggshell and monitored. Headstart chicks were then located and measured approximately every three days (2.88 ± 1.37). During each visit, chicks were examined for any evidence of physical damage from the transmitters. I also measured body mass with a spring scale (± 1 g) and length of tarsus, culmen, skull and wing chord with calipers (all to ± 1 mm). Glue was added to the transmitter on visits when the transmitter appeared loose. When a transmitter fell off, we attempted to relocate the chick and reattach the transmitter. If a chick died, we attempted to locate its remains and searched the area to determine the cause of death. All chicks were monitored until they were considered "fledged" at 35 days or when observed in flight.

Control chicks were not radioed but monitored by searching shell rakes approximately every three days (3.26 ± 1.9). If a chick was not found on the shell rake during two consecutive visits, pairs would be monitored at a distance until either (a) chicks were observed, or (b) adult behavior after an extended observation period indicated that chicks were no longer present. If chicks were found, they were inspected to assess health but regular growth measurements were not taken. As with headstart chicks, all control chicks were monitored until they were considered "fledged" at 35 days or when observed in flight.

Statistical Analysis

The Mayfield Method (Mayfield 1961) was used to calculate the rates of nest survival and probabilities of a nest surviving from egg laying to the hatch date for all nests. This method was also used to calculate the rates of chick survival and the probability of a nest having a chick survive to fledge. Daily survival rates of nests and broods were calculated as [daily survival rate = 1 – (total number of failures / total number of exposure days)], where exposure days equal the number of days the nest or chicks were monitored. To calculate the probability of a nest surviving for the entire egg-laying to incubation period, I raised the daily survival rate of that period to an exponent equal to the number of days needed to complete the nesting stage (i.e., 27 days for incubation, 35 days during chick-rearing to fledge). The probability of success of one egg headstart clutches (i.e. nests without a real egg left in the scrape) was also calculated using Mayfield daily survival rate to assess whether or not breeding pairs with one artificial egg clutches abandoned at the same rate as all headstart nests.

I modeled daily survival rate of oystercatcher nests using logistic-exposure models (Schaffer 2004) in SAS (PROC GENMOD). This method allowed me to examine the relationship between nest survival and multiple explanatory variables. I chose to use the logistic-exposure model because it does not assume homogeneous daily survival rates among or within nests (Schaffer 2004).

The logistic exposure models included a subset of the following nest-, local-, and time-specific explanatory variables: year (2010 or 2011), site (AICW or Southwest Bulls Bay), nest age, date (represented as the day in the nest season with April 1st as day 1) and tide height (maximum during interval between visits). Separate models were run for headstart and control nests for both incubation and chick rearing. Parent type (original, foster or mix parents with a combination of both real and foster chicks) was added to the headstart chick survival model to determine if parent type had an effect on brood survival. In addition, a model was run to investigate factors that might influence the survival of the original eggs that were left in headstart nests. Nests with one egg clutches where no original egg was left in the scrape (n=14) were not included in that analysis. Occasionally, nests failed before I was able to collect the eggs from a complete clutch.

This happened with 17% (n=14) of the assigned headstart nests. These nests were included in the analysis of the daily survival of original eggs but omitted from the analysis of daily survival for headstart nests with artificial eggs.

A mixed model (PROC GLIMMIX) was used to analyze the hatch success of the collected eggs in the incubator. Site (AICW or SWBB), year (2010 or 2011), collection date, weight and volume were included as explanatory variables. An analysis of variance was used to assess if there were differences between the weight and volume of collected eggs between both sites and years.

As part of pilot study to investigate the use of highly accurate GPS to measure elevation of shell rakes, I conducted a separate analysis to assess the relationship between nest success and both elevation and slope at a subset of nests during the 2011 breeding season. Elevation surveys were conducted at 49 nests on 24 May 2011 and at 24 nests on 23 July 2011. Measurements taken on the second date included nests that had not been initiated or measured on the first date. Nests were surveyed using Real Time Kinematic (RTK) GPS. Tidal benchmarks were not available near the nests and new benchmarks were established near the nests in Southwest Bulls Bay and near the nests on the AICW. Benchmarks were established by securing a 1.3m angle iron into the shell bank. Each benchmark was occupied by a Trimble Model 5700 dual channel receiver attached to a Trimble Zephyr antenna. Benchmark location and elevation was corrected using OPUS Static or Rapid Static corrections. Each nest site was visited and GPS measurements were made of the nest, high point near the nest, low point of the slope, and water level. Readings were taken with a Trimble Model 5800 receiver and recorded on a Trimble Survey Controller. Point data were taken only when “RTK fixed” conditions were met and RMS (i.e., root mean square) errors of the fix were < 1 cm horizontal and 2 cm vertical (i.e., this is the RMS error of the fix, not necessarily the accuracy of the data itself). Separate models were run using a general linear method (PROC GLM) to determine whether slope or elevation had an impact on hatch or fledge success. An analysis of variance was run for all slope and elevation measurements to investigate if there were differences in elevation or slope for either nest type or site.

For all analyses alpha was set at 0.10, although I report actual *P*-values throughout. Mean estimates are presented ± 1 standard deviation and coefficient estimates are presented ± 1 standard error unless otherwise stated. All analyses were conducted using SAS version 9.3 (SAS Institute, Cary, North Carolina).

RESULTS

Nesting Cycle

The duration of nesting activity (time from initiation of first nest until the last nest or chick failed to hatch or fledge) in 2010 and 2011 was 119 days. In 2010, the first nest was found (and likely laid) on 5 April along the waterway and on 6 April (laid *ca.* 2 April) in Bulls Bay, and the last nests were initiated on 13 June along the waterway and 11 June in Bulls Bay. In 2011 the first nests were found and likely laid on 4 April along the waterway and 17 April in Bulls Bay, and the last nests were initiated on 2 June along the waterway and 15 June in Bulls Bay.

For the 2010 and 2011 breeding season combined, 55 control nesting attempts were monitored along the AICW, 35 control nesting attempts were monitored in Southwest Bulls Bay, 53 headstart nesting attempts were monitored along the AICW, and 31 headstart nesting attempts were monitored in Southwest Bulls Bay (Figure 2.3). Twenty-five pairs were assigned to the control group in 2010 and 21 in 2011 (Table 2.1). Twenty-seven pairs were assigned to the headstart group in 2010 and 23 in 2011 (Table 2.2). Replacement clutches were common when parents abandoned nests or when nests were lost to overwash or depredation. For example, 25 control pairs made 49 nest attempts in 2010 and 21 control pairs made 41 nest attempts in 2011 (Table 2.1). In 2010, 26 headstart pairs made 47 nest attempts, and 23 headstart pairs made 37 nest attempts in 2011 (Table 2.2).

Incubator Success

In 2010, 53 eggs were collected from 39 clutches between 14 April and 14 June and 38 eggs were collected from 32 clutches between 17 April and 12 June in 2011. There were no significant differences between the weight (44.21 ± 3.85g) or volume (43.22 ± 3.64cm^3) of the eggs collected between sites and years ($F_{1,20} \leq 2.19$, $P \geq 0.15$ for each). Hatching success for eggs in the incubator was 62% in 2010 and 84% in 2011. Hatching success in the incubator was significantly affected by year ($F_{1,17}$ =6.8, P=0.02) but not by site, collection date, mass or volume ($F_{1,68} \leq 2.45$, $P \geq 0.12$ for each). The odds of an egg hatching in the incubator in 2011 were 5.7 times greater than the odds of an egg hatching in the incubator in 2010**.**

Nest Fate

Apparent success of control nests was <20% for both sites and years (Table 2.1). Approximately 10 – 80% of control nests were depredated among sites and years while 0 – 30% of nests were overwashed (Figure 2.4). The camera system recorded 9 nest depredation events at control nests in Southwest Bulls Bay during the 2011 breeding season (n = 8 raccoon [*Procyon lotor*], n = 1 American mink [*Neovison vison*]).

Apparent success of headstart nests (i.e., parents continued to incubate until ≥ 1 chick was placed at nest or original egg hatched) ranged from 35 – 57% for both sites and years (Table 2.2). Less than 20% of nests failed due to predation or overwash in each site and year. (Figure 2.5). Abandonment occurred in Southwest Bulls Bay in 2010 and slightly less frequently along the AICW in 2011. Approximately 20% of headstart nests failed before eggs could be collected from the AICW in either year and in Bulls Bay for the 2010 season. However, the proportion of headstart nests that failed before collection for the Southwest Bulls Bay area decreased to 7% for the 2011 breeding season.

Excluding nests that failed before eggs could be collected (17%, n=14), only 10% (n=7) of nesting attempts had an original egg survive until the hatch date. Estimates of nest survival from Mayfield calculations (Table 2.3) appeared very similar to estimates of apparent nest success (Table 2.1 and 2.2). The probability of success for control and headstart nests across both sites and years was 10% and 52%, respectively (Table 2.3).

The model combining all nests indicated that nest type (headstart or control) was the only significant variable influencing nest survival (χ^2_1=58.19, $P < 0.0001$). The odds of a headstart nest surviving was 6.2 times the odds of a control nest surviving. In the model investigating the survival of control nests only, the day in the nest cycle (nest age) was positively related to nest success (χ^2_1=2.63, P=0.10). For every day a nest survived on a given site, it was 1.03 times more likely to hatch. The opposite was found in the headstart nest model where the day in the nest cycle was negatively related to nest survival (χ^2_1=6.03, P=0.01).

High tide was the only other variable in the control nest model that was significantly related to nest survival (χ^2_1=4.74, P=0.03). For every meter increase in high tide, a control nest was 1.9 times more likely to fail. Unlike control nests, headstart nest survival was not significantly related to tide height (χ^2_1= 2.04, P = 0.15). Day in season (date), site, year, or a combination of site and year also were not significantly related to survival rates of control or headstart nests ($\chi^2_1 \leq 2.17$, $P \geq 0.14$ for each). However, there was a significant relationship between year and survival of original eggs in headstart nests (χ^2_1 = 6.10, P=0.01) and between day in the nesting season and survival of original eggs in headstart nests (χ^2_1 = 3.61, P = 0.06). The odds of an original egg surviving to hatch in 2010 was 2.95 times the odds of an original egg surviving to hatch in 2011. For every day increase in the breeding season, original eggs were 1.01 times more likely to fail. Headstart nests without an original egg (i.e. one egg clutches) had a higher probability of success (0.66) compared to all headstart nests.

The model investigating the effect of slope and elevation on nest success indicated that slope and elevation were not related to nest success. Elevations of nesting territories between the two study areas ranged from 0.34m – 1.57m (Figure 2.6). Elevation of all nests with measurements (n = 72) averaged 1.25 ± 0.21 m and slope for all nests sites with measurements (n = 62) averaged 17.64 ± 10.15%. There were no differences in elevation for nest type, site or their interaction (model $F_{3,67}$ = 2.00, P = 0.12). Slope differed between study sites ($F_{1,58}$ =17.96, P < 0.0001) but not between nest types ($F_{1,58}$ =0.73, P = 0.40) or an interaction of the two ($F_{1,58}$ = 0.06, P = 0.81). The slope of nesting shell rakes along the AICW (21.45 ± 9.39%) was steeper compared to nesting shell rakes in Southwest Bulls Bay (11.20 ± 8.01%).

Chick Survival

A total of 24 chicks hatched from control nests and 58% (n=14) survived to fledge (35 days or when observed in flight). A total of 60 chicks were placed into 44 headstart nests and 22% (n=13) survived to fledge. When data were pooled among sites, years, and nest types (both headstart and control), 32% (n=27) of all chicks monitored were resighted at fledging age.

During the chick-rearing stage of the nesting cycle, both control and headstart chicks had low survival in Southwest Bulls Bay (n=1 control chick surviving to fledge in

2010 and n=2 headstart chicks surviving to fledge in 2011). Therefore, I pooled headstart and control nests along the AICW to investigate if there was a difference between survival of headstart and control broods. Results from this model indicated that a control brood along the AICW had a better chance of having a chick survive to fledging age than a headstarted brood ($\chi^2_1 = 3.24$, $P = 0.07$). The odds of a control brood surviving to fledge were 3.98 times the odds of a headstart brood having at least one chick survive to fledge. Mayfield daily survival estimates for headstart and control broods are presented in Table 2.4. The probability of a control brood having at least one chick survive to fledge was 83% while the probability of a headstart brood having at least one chick survive to fledge was 18%.

Survival of control broods was not significantly affected by age, the day in the season (date), tide, or year ($\chi^2_1 \leq 2.35$, $P \geq 0.13$ for each). Site effects could not be assessed because the sample size for control broods in Southwest Bulls Bay was low (n=1; that chick fledged). There was, however, a significant site effect for headstart broods ($\chi^2_1 = 9.79$, P=0.002). A headstart brood along the AICW was about 3 times more likely to fledge than a brood in Bulls Bay. The age of the brood also significantly related to survival ($\chi^2_1 = 19.98$, P <0.001). The odds of a brood surviving increased by 1.1 times for every day it survived. Headstart brood survival was not influenced by the day in the nest season (date), parent type (real, foster or mix), high tide, year or a combination of site and year ($\chi^2_1 \leq 0.98$, $P \geq 0.32$ for each). Chicks that were headstarted (i.e., returned) returned to their original parents (n=28) were accepted in 97% of cases, chicks that were headstarted to foster parents (n=9) were accepted in 89% of cases, and chicks that were headstarted to foster parents along with original chicks (i.e., mix parents, n=7) were accepted in 86% of cases. All chicks that were not accepted by parents (regardless of parent type) displayed deformities occurring from incubator errors in the 2010 season.

Of the headstart chicks that did not survive to fledge, 74% (n=35) were lost within the first week after they were returned to their original or another suitable headstart nest (Table 2.5). Causes of chick loss were often difficult to assess because remains and signs of loss were not often observed on nesting territories. Identifiable causes of chick loss included predation (n=5), killed by adults (n=6) and starvation or poor health (n=2).

I assessed the relationship between brood survival and elevation and slope of the nesting shell rake. The relationship of slope and elevation on fledge success of headstart chicks could not be evaluated for Southwest Bulls Bay because of the small sample size of nests that had at least one chick in the brood survive to fledge that in this study area (n=1). Both slope and elevation were significantly related to the brood success of headstart nests along AICW ($F_{1,8}$= 5.81, P = 0.04 and $F_{1,8}$ = 8.26, P = 0.02, respectively). There were no control chicks fledged in Bulls Bay in 2011. I also combined all nest types (headstart and control) to investigate the effect of slope and elevation on all nest sites with slope and elevation measurements along the AICW. Slope ($F_{1,11}$ = 4.60, P = 0.06) and elevation ($F_{1,11}$ = 5.81, P = 0.03) were significantly related to brood survival along AICW. Slope was lower for nesting locations along the AICW that fledged ≥ 1 chick (18.8 ± 7.3% for successful nests and 25.5 ± 5.2% for failed nests) and elevation was higher for nests that fledged ≥ one chick (1.3 ± 0.09 m for successful nests and 1.1 ± 0.3 m for failed nests).

DISCUSSION

Nest and brood success of American Oystercatchers in the Cape Romain Region was highly variable among sites and years, a pattern that appears to be common in the Southeastern U.S. (Sabine et al. 2006; Thibault 2008). The nest success (11%) and fledging rate (0.30 chicks per pair) of control nests during this study appears similar to results reported for another two-year study on the reproductive success of American Oystercatchers within the Cape Romain Region (15% nest success and 0.25 chicks per pair; Thibault 2008). In addition, studies conducted in other mid-Atlantic states reported comparable findings. An eight-year study on barrier beaches in North Carolina reported 24% nest success and 0.19 chicks fledged per pair (McGowan 2004) and a four-year study on several coastal islands in Virginia found 14% mean nest success and 0.24 chicks fledged per year (Nol 1989).

Reproductive success in American Oystercatchers tends to be low throughout the southeastern U.S. (Nol 1989; Davis et al. 2001; George 2002; McGowan 2004). With the use of headstarting, nest success of American Oystercatchers nesting within the CRR was enhanced to 52% (compared to 10% for control nests). The nest success of headstart nests surpassed the nest success of Oystercatchers nesting in Georgia (38%), one of the highest documented hatch rates of pairs nesting in the southeast (Sabine et al. 2006). Although nest success was higher in headstart compared to control nests during our study, fledge success for headstarted nests remained low (0.26 chicks per pair).

High variability in nest success both within and among sites and years within the CRR suggests factors at local scales such as disturbance, predation and overwash events likely influence nest success of American Oystercatchers more so than regional factors such as weather or food availability. In my study, reproductive success also varied between study areas, with higher success achieved along the AICW compared to the Southwest Bulls Bay. This was contrary to the findings of previous research conducted within the same study areas within the Cape Romain Region (Thibault 2008). Reproductive success within the CRR was also variable between years. Reproductive success was highest in the 2006 and 2008 breeding season (0.43 chicks fledged per pair for each year) and lowest in the 2007 breeding season (0.04 chicks fledged per pair) for both sites (J. Thibault unpublished data, Thibault 2008). During my study, reproductive success was higher for both sites in the 2010 breeding season (0.31 chicks fledged per pair) and slightly less for the 2011 breeding season (0.25 chicks fledged per pair). While reproductive success in American Oystercatchers varies between sites and among years, it is unknown if these levels of annual productivity are adequate to maintain the population (Davis et al. 2001).

Incubator Success

Although I successfully collected, incubated and hatched American Oystercatcher eggs, I did encounter some difficulties with incubation. During an earlier pilot study, 39 eggs were collected from AICW and Bulls Bay and eggs were returned to the nest when eggs showed indications of hatching (i.e., pipping, starring) or within 2 hours after hatching (J. Thibault unpublished data). The pilot study found that the majority of collected eggs with known hatch fate did not hatch successfully (n=20, 59%) either in the incubator or after being returned to the nest. Because this pilot study reported that there were also eggs with unknown hatch fate (n=5) after being returned to the nest I chose to return chicks to nests immediately after hatch in order to more accurately assess hatch success in the incubator. In the first year of my study, hatch success for incubated eggs was 60%. In contrast, hatching success during 2011 was 100%. Poor hatching success in 2010 included both unhatched eggs and eggs that hatched but with deformed chicks (e.g. ectopic viscera, splay legs). Two factors appeared to contribute to poor hatching success. First, the air-conditioning unit in the facility that housed the incubator malfunctioned. Although the incubator internally regulated the temperature, it appeared to be important that the external temperature remain relatively stable as well. This malfunction was fixed within 24 hours but its state of disrepair was coincident with several eggs hatching deformed chicks or failing to hatch. Second, humidity and temperature levels within the incubator appeared to be set at less than ideal levels during the early breeding season of 2010. The initial temperature was set at 37.6°C and humidity at 50% (60% during hatch), following recommendations for poultry eggs. Deformities occurred with these settings. When the temperature was lowered (as low as 37.2°C), chicks did not display the aforementioned deformities and hatching occurred at a much higher rate. Before resuming headstarting for American Oystercatchers during the 2011 breeding season, I tested the incubator using 36 chicken eggs. The incubator was set at 37.6°C and humidity at 50% humidity during development. Eggs were transferred to a separate Styrofoam incubator with temperature settings at 37.6°C and humidity at 65% when eggs were hatching. All of the fertile eggs that were expected to hatch did hatch out healthy chicks without deformities, regardless of placement of the eggs within the incubator or order of placement. A study by Powell et al. (1997) on captive rearing of piping plovers indicated that it was possible to successfully incubate shorebird eggs artificially with settings at 37.4°C and between 78-82% humidity. Therefore, I decreased the incubator temperature to 37.4°C and increased humidity to no lower than 65% for eggs collected in 2011. This change resulted in 100% hatch success of all fertile eggs collected and all chicks hatched healthy.

Nest Survival

Apparent nest success can overestimate survival because successful nests have a higher rate of detection than failed nests (Johnson & Shaffer 1990). During this study, however, estimates of apparent nest success for both headstart and control nests were similar to Mayfield estimates. This may be because of the frequency of nest searches and the visibility of oystercatcher nests on shell rakes. Oystercatcher nests were easily located at my study locations and 3 day intervals of nest checks appeared to be adequate to estimate hatching success. Nests were found as they were laid and unsuccessful nests were accounted for with the same frequency as successful nests. Because of higher detection of nests, the apparent nest success estimate may not have overestimated hatching success therefore yielding similar results as the Mayfield method.

Hatching success and nest survival were higher for control nests along the AICW compared to those in Bulls Bay for both years. This is different from results reported for the 2006 breeding season for these sites (Thibault 2008) but was similar to results found during the 2008 breeding season (J. Thibault unpublished data). Results from the 2006 season showed that nests along the waterway appeared to fail from overwash, depredation, abandonment, failure to hatch and human disturbance while nests in Bulls Bay failed predominantly from depredation or overwash events (Thibault 2008). With little documentation of mammalian predation during the 2006 breeding season, it appeared that nests in Bulls Bay were more successful compared to those on the Waterway because of the lack of anthropogenic disturbance. Headstart nests (i.e., the nest structure with artificial and original eggs, not survival of eggs in the incubator) experienced higher nest success and survival along the AICW compared to Bulls Bay in 2010 but not in 2011 (Tables 2.2 & 2.3). It appears that in 2010 artificial eggs were less secure and were often removed by predators or flooding and this coincided with parental abandonment. During the 2011 breeding season, all artificial eggs were secured in the scrape with a longer anchor and I did not observe missing artificial eggs and subsequent parental abandonment at all. Because there is less anthropogenic disturbance (i.e. overwash from boats) within the Southwest Bulls Bay, breeding pairs are less likely to abandon artificial eggs and therefore are more likely to continue to incubate until chicks could be returned.

While the odds of a control nest succeeding increased for every day the nest survived, the opposite was observed for headstart nests. This opposite effect observed between nest age and survival between headstart and control nests may be explained by the ability of artificial eggs to ‘survive’ despite the quality of a nest site or events that occur there. For example, control nests located on a less suitable nesting territory within a study area (e.g. prone to overwash or predation) may be more likely to fail earlier in the nesting cycle. For the Cape Romain Region, there appear to be many factors that can contribute to nest loss and often nest locations within and between both sites experience poor survival. Headstart nests change this dynamic through the use of artificial eggs. Even in less suitable locations, nests are able to survive overwash and depredation attempts but repeated overwash and depredation can ultimately force adults to abandon nests when the risk of incubating the nest outweighs the benefit of hatching. Therefore, headstart nests may be more likely to be abandoned over time.

Tide height was a significant factor influencing the survival of control nests. The southeastern U.S. is prone to tropical storms and hurricanes that can result in high levels of nest loss for many avian species that breed in low-lying habitats such as beaches or marshes. For example, Thibault (2008) reported that the majority of American Oystercatcher nests within the Cape Romain Region that failed during the 2007 breeding season were lost to overwash created by two tropical storms that occurred during May and June. Although no nests in the CRR were affected by tropical storms or hurricanes during the breeding season in either year during this study, high nest loss occurred during extreme spring high tides on 26 May 2010 and 16 April & 14 May 2011. It appears that nests in the CRR are prone to natural overwash events due in part to the physical structure of the shell mounds used as nesting habitat. Tide levels during spring can be extreme (e.g. highest records for the 2010 and 2011 breeding seasons were 3.02 and 3.07 meters, respectively) and often leave only the top portion of shell mounds exposed. Other studies investigating nest loss of oystercatcher species have also found that nest loss can occur more frequently in locations that are vulnerable to tidal flooding (Lauro & Burger 1989; Nol 1989; Lauro & Nol 1993). The effect of high spring tides can be exacerbated by boat wakes especially along the waterway where boat traffic can be frequent and the intensity of the wakes can be severe. American Oystercatchers demonstrate nest site fidelity and pairs within the CRR that lost nests continually re-nested at the same spot on a shell mound even if the nest elevation was prone to flooding. Interestingly, nest elevation was not found to significantly influence the survival of control nests for this study but this could be explained by the low variation between nest elevations for nests with measurements (approximately 80% of nesting territories with measurements had elevations between 1-1.5 meters; Figure 2.6). Through the use of headstarting, nest survival was no longer significantly affected by tide height. Strings attaching artificial eggs to anchors held eggs in place despite the severity of overwash. Even nests that experienced overwash events that were so severe that shell and wrack buried artificial eggs had occurrences of adults digging out eggs, reforming a scrape and continuing to incubate the artificial eggs.

Nest Fate

Differences in reproductive success between sites and years appeared to be due to differences in overwash and predation. Identification of predators on shell rakes for both study sites proved difficult because tracks were not visible on the shell substrate. It was common to find a failed nest with no eggshells or evidence of depredation. Although I was often unable to determine the cause of nest failure of control nests for either site and year, overwash appeared to be the primary cause of identifiable failure along the AICW for both years while predation appeared to occur frequently within Bulls Bay in both years. Furthermore, camera surveillance allowed me to determine that predation was common in Southwest Bulls Bay in 2011, accounting for 80% of nest loss for control nests. Raccoons were identified as the most common nest predator, accounting for 89% (n=8) of recorded nest depredation events. Other studies investigating nest predators of American Oystercatchers found that raccoon were responsible for a significant amount of nest loss (McGowan 2004, Sabine et al. 2006). American mink were also identified as a nest predator within this area (n=1 recorded event). Mammalian nest depredation within these study areas was rarely documented in past years (Thibault 2008). Another noteworthy finding from camera surveillance was that depredation events occurred before overwash events which indicates that nests that failed with signs of overwash and no signs of depredation could be falsely listed as overwash as the cause for nest loss.

Failure of headstart nests was typically attributed to repeated overwash or depredation attempts that ultimately caused adults to abandon. A significant amount of headstarted nests failed before the clutch was complete and eggs could be collected. Occasionally it was difficult to assess whether the cause of failure was overwash, predation or a combination of the two stressors because adults would be observed incubating artificial eggs after overwash or predation events had occurred. However, it is possible to speculate on the fate of some headstart nests. Artificial eggs were painted prior to being secured in nest scrapes so scratch or bite marks could be used to identify possible nest depredation. In addition, at the start of the 2010 breeding season 6” nails were used to secure artificial eggs into nest scrapes but were often pulled up and found in the marsh with bite and scratch marks. Evidence of depredation (scratch, teeth marks or eggs being pulled up) on artificial eggs was identified for 29% (n=24) of headstart nests and overwash evidence was observed at 33% (n=28) of headstart nest sites for both sites and years. Evidence of attempted depredation or overwash did not necessarily influence the ultimate fate of headstart nests because of the use of artificial eggs (see Figure 2.5). Original eggs were additional indicators of headstart nest fate, with only 8% (n=7) of headstart nests having an original egg survive until the hatch date.

Chick Survival

For the 174 nesting attempts (headstart and control) monitored during the two years of this study, only 27 chicks fledged and approximately 89% of these fledged from the AICW. Although headstarting may improve nest success during incubation, it did not appear to ultimately enhance productivity. Brood success and productivity were higher for control and headstart nests along the AICW compared to those in Bulls Bay for both years. Chick survival was also lower in Southwest Bulls Bay compared to the waterway. Of the headstarted chicks that did not survive to fledge in Bulls Bay, 95% died within the first week after they were placed in the nests (Table 2.5). In contrast, only 59% of headstarted chicks placed along the AICW that did not survive to fledge were lost within the first week after they were placed in the nests. Differences in survival and fledging success between Bulls Bay and the waterway may be attributed to the differences in site quality (i.e. food availability, increased rates of predation or overwash, or closeness to neighbors).

Control broods appeared more likely to have at least one chick survive to fledging age than headstart broods. However, only 29% of all chicks monitored were control chicks. Control nests that produced chicks may have been located where pressure from predation, overwash or other extrinsic factors was low and as such chick survival may also be higher there. All headstart nests that had an original egg survive to hatch were also able to fledge a chick (headstart or original). Territories that did not have an original egg survive to hatch often did not fledge chicks. Parents on these nesting territories were confirmed to accept released chicks and therefore it was likely that these nesting territories were not as suitable to longer term chick survival due to factors such as predation, overwash or other extrinsic pressures.

Headstart nests provided information on the differences in brood survival between the two study areas. Investigation of the differences in site quality was necessary to try to assess why chicks located along the AICW were more likely to fledge than those located in Bulls Bay. When chicks were lost, I searched the shell rake and/or used telemetry to locate remains or clues that may help determine the cause of loss. I was unable to locate transmitters and/or remains for the majority of chicks monitored that were lost (n=30). Occasionally, transmitters were found but no remains were observed (n=15). I was only able to find remains for 14% (n=8) of all chicks that did not survive to fledge. A low number of headstart chicks were rejected and killed after they were released (n=4) and all of these chicks were from the 2010 breeding season and displayed deformities after hatching in the incubator. Because the majority of breeding pairs accepted and brooded chicks after they were returned despite parental type (i.e., original, foster or mix parents), it was evident that there were other driving factors in chick loss for these areas. Research has found that predation and starvation are the two major causes of chick loss (Nol 1985) and studies have reported other oystercatcher pairs killing chicks (Sabine et al. 2006). I investigated these possible stressors for the two study areas and attempted to determine the leading causes of chick loss within and between sites.

A study by Ens et al. (1992) reported that nesting areas adjacent to feeding areas fledged more chicks than nesting areas separated from feeding areas by distances of 200-

500m. However, it has also been reported that for individuals that breed in areas with abundant prey the cost of food transport may be negligible (Ens et al. 1992). The latter scenario may be common in the CRR where there appears to be an abundance of food for breeding and non-breeding oystercatchers (Hand 2006; Thibault 2008). All of the chicks in this study observed with signs of starvation or poor condition occurred at the end of the breeding season (July 4-11) when parental attentiveness may decrease as there is more of an energetic risk of survival to adults if they extend brood care too long (Rutherauff et al. 2009). Therefore, it appears that chick starvation is not the leading cause of chick loss within and between these areas.

Avian predation or predation on chicks by other breeding pairs could be a cause of chick loss in my two study areas. Thibault (2008) reported that avian predation was a cause of nest loss during incubation, although I did not observe any signs of avian predation on nests that failed during this study. However, I did observe remains of chicks that displayed signs of avian predation (i.e., stab wounds on body). All of these observations (n=4) occurred on shell rakes that were shared with other breeding pairs. It is likely that at nesting locations where breeding pair territories are close or overlap, adjacent pairs may kill chicks (Sabine et al. 2006). Because the majority of pairs nesting within the CRR defended a single shell rake, chick loss from adjacent pairs was not likely to be a major cause of chick loss for these study areas.

A study on the reproductive success of shorebird species reported that the greatest influence on reproductive success was fluctuating annual predation pressure (Smith et al. 2007). All territories within the CRR are adjacent to abundant salt marsh, which serves as suitable habitat for mammalian predators such as raccoon and American mink. Camera surveillance in Southwest Bulls Bay during the 2011 breeding season indicated that mammalian predation occurred regularly during incubation. If mammalian predation was a major cause of chick loss for this area and along the AICW, I would expect that chick remains would rarely be found and chicks would be more likely to fail within the first few days after hatch when they are less mobile. For this study, chick remains were not found 79% of the time and 97% of transmitters that were recovered after chick loss were in or near the nest scrape. There were a few instances where the use of transmitters helped identify mammalian predation as the cause for chick loss. For example, one transmitter was recovered near the den of a female mink with kits and another transmitter from an older chick was tracked behind the shell rake in the marsh and was found near mink scat and the bands of the missing chick.

There were frequent observations of American mink during the daytime near nesting locations in Bulls Bay and many scrapes were observed throughout nesting territories without eggs during the early 2011 breeding season. Trapping efforts for mammalian predators (6 April-12 April, 2011) along the marsh adjacent to a large shell rake south of Venning Creek where three pairs of oystercatchers had established nesting territories (two headstart pairs and one control pair) resulted in the removal of 8 American mink. Camera surveillance on the control nests present on this shell rake recorded nest depredation events by raccoon. This in combination with scratch and bite marks on artificial eggs made it evident that raccoon were a frequent predator on this shell rake. Despite raccoon being a known nest predator, two chicks released into a headstart nest on this rake survived to fledging age. This suggests that although raccoon may be a common nest predator in Bulls Bay they may not be efficient predators of chicks. Mink predation can be difficult to detect and may require additional investigation to determine the extent to which they are responsible for nest and chick failure (Craik 2010).

Slope and elevation of nesting shell rakes also were related to chick survival of headstart chicks located along the waterway. Chicks on territories with decreased slope or increased elevation were more likely to fledge. A study by Hazlitt (2001) also reported that slope had a significant impact on the reproductive success of oystercatchers. Chick loss in this study area was occasionally coincident with signs of overwash (n=3) which can be influenced by elevation or slope.

Investigation on the parental acceptance of headstarted chicks indicated that adults were as likely to accept foster chicks as original chicks. Two determining factors on whether or not parents accepted headstarting chicks appeared to be whether chicks were healthy (i.e. no deformities) and if the chick was returned around the estimated hatch date. Adults were observed killing chicks with significant deformities (splay legs or ectopic viscera) in the 2010 breeding season. The only occurrence of adults rejecting and killing chicks during the 2011 breeding season was an instance when chicks were returned to a headstart nest before the anticipated hatch date.

Conclusions

Headstarting can be an effective tool for enhancing the nest success of American Oystercatchers. However, headstarting may not ultimately be effective if the majority of chicks released onto nesting territories do not survive to fledging age. Fledge success within this area remained low and variable due at least in part to predation. Headstarting may be most appropriate where flooding, overwash, or disturbance are the primary causes of nest loss. If headstarting were to be considered as a management strategy to enhance the productivity of oystercatchers within the CRR, our data suggest that more detailed data on predation rates, timing of predation during the oystercatcher breeding season, and population sizes of predators are needed to determine if headstarting could enhance productivity or if predator removal were needed. For example, a study on the long-term effects of North American mink on seabirds in western Scotland found that colonies and breeding pairs decreased by up to 52% over ten years in locations where mink were present (Craik 2010). In areas with high predation rates, predator control can increase the reproductive success of American Oystercatchers but can be labor intensive, long-term and expensive (McGowan 2004), and requires a detailed understanding of the ecology, diet, movement patterns, and population dynamics of the predators.

Although this study monitored chicks until fledge age, it would be beneficial to monitor chick survival post-fledge. While fledging success is the metric to determine productivity, I occasionally did not observe chicks after their fledge date suggesting that mortality occurs after 35 days post hatch. Because of Oystercatcher's specialized diet, chicks are unable to obtain food on their own and rely on parents to provision them for up to 60 days after hatching (Nol and Humphrey 1994). Further study on chick survival post-fledge is needed to accurately estimate fecundity and provide information of the sources of chick mortality and other habitat related factors that affect survival during this stage.

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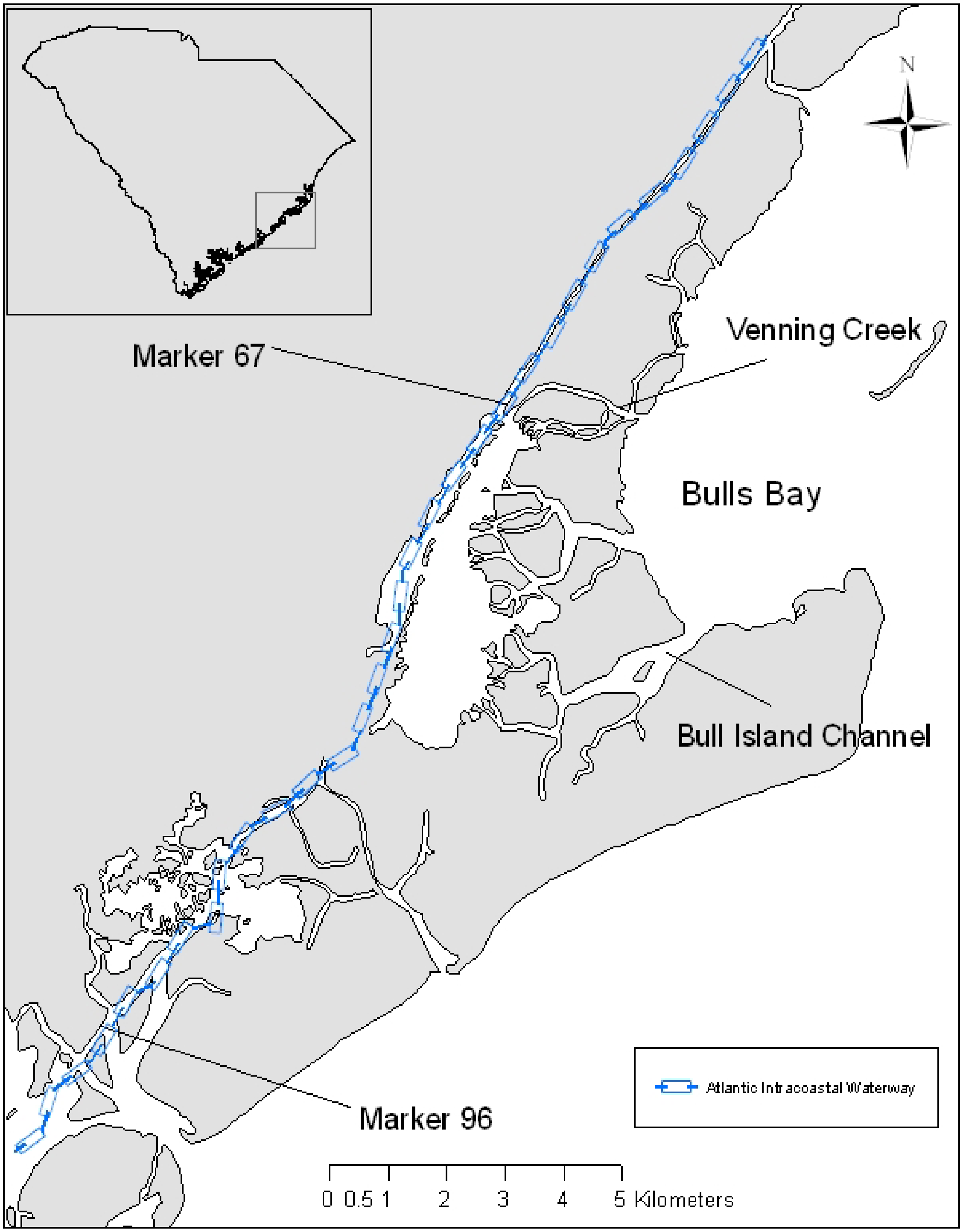

Figure 2.1. Study area within the Cape Romain Region, South Carolina. Study nests occurred along the Atlantic Intracoastal Waterway between markers 67 and 96, and in Bulls Bay between Venning Creek and the Bull Island Channel.

Figure 2.2. Camera set-up for control nests in Southwest Bulls Bay April-June 2011 in Cape Romain National Wildlife Refuge, South Carolina.

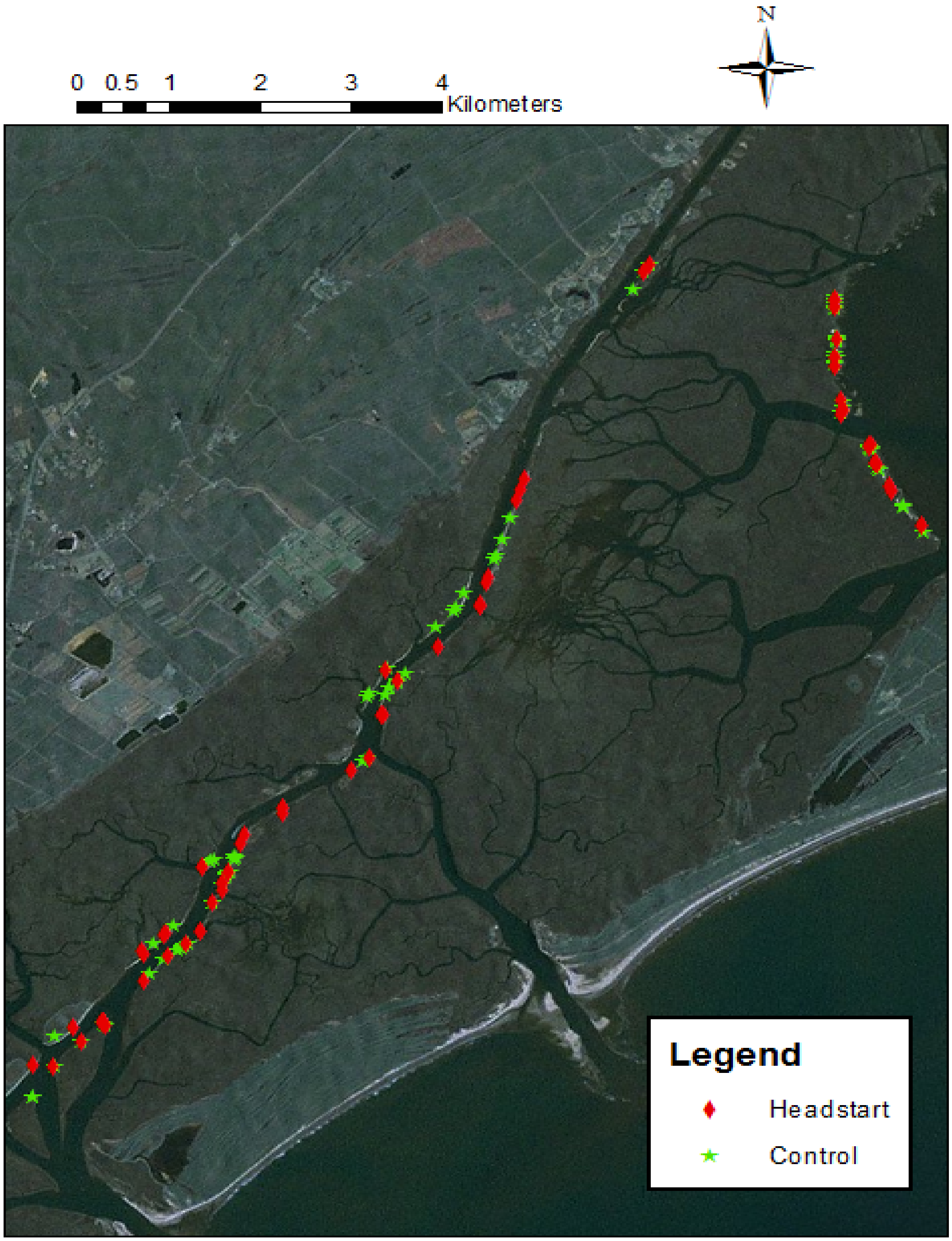

Figure 2.3. Assigned headstart and control nests of American Oystercatchers in the Cape Romain Region of South Carolina during the 2010 and 2011 breeding season.

Table 2.1. Reproductive success of control pairs of American Oystercatchers within the Cape Romain Region, South Carolina, 2010 & 2011.

Year	Site	No. pairs	No. nest attempts	Apparent nest success, ≥1 egg hatched (%)	Brood success, ≥1 chick fledged (%)	No. fledglings	Productivity estimate[1]
2010	Atlantic Intracoastal Waterway	17	31	6 (19)	6 (100)	8	0.47
	Southwest Bulls Bay	8	18	1 (6)	1 (100)	1	0.13
2011	Atlantic Intracoastal Waterway	13	24	3 (13)	2 (75)	5	0.38
	Southwest Bulls Bay	8	17	0 (0)	0 (0)	0	0.00
	TOTAL	46	90	10 (11)	9 (90)	14	0.30

[1] **Number of young fledged/ number of pairs**

Table 2.2. Reproductive success of assigned headstart pairs of American Oystercatchers within the Cape Romain Region, South Carolina, 2010 & 2011.

Year	Site	No. pairs	No. nest attempts	Apparent nest success, ≥1 chick returned (%)	Brood success, ≥1 chick fledged (%)	No. fledglings	Productivity estimate[1]
2010	Atlantic Intracoastal Waterway	18	30	17 (57)	7 (41)	7	0.39
	Southwest Bulls Bay	9	17	6 (35)	0 (0)	0	0.00
2011	Atlantic Intracoastal Waterway	14	23	11 (48)	4 (36)	4	0.29
	Southwest Bulls Bay	9	14	10 (71)	1 (10)	2	0.22
	TOTAL	50	84	44 (52)	12 (27)	13	0.26

[1] Number of young fledged/ number of pairs

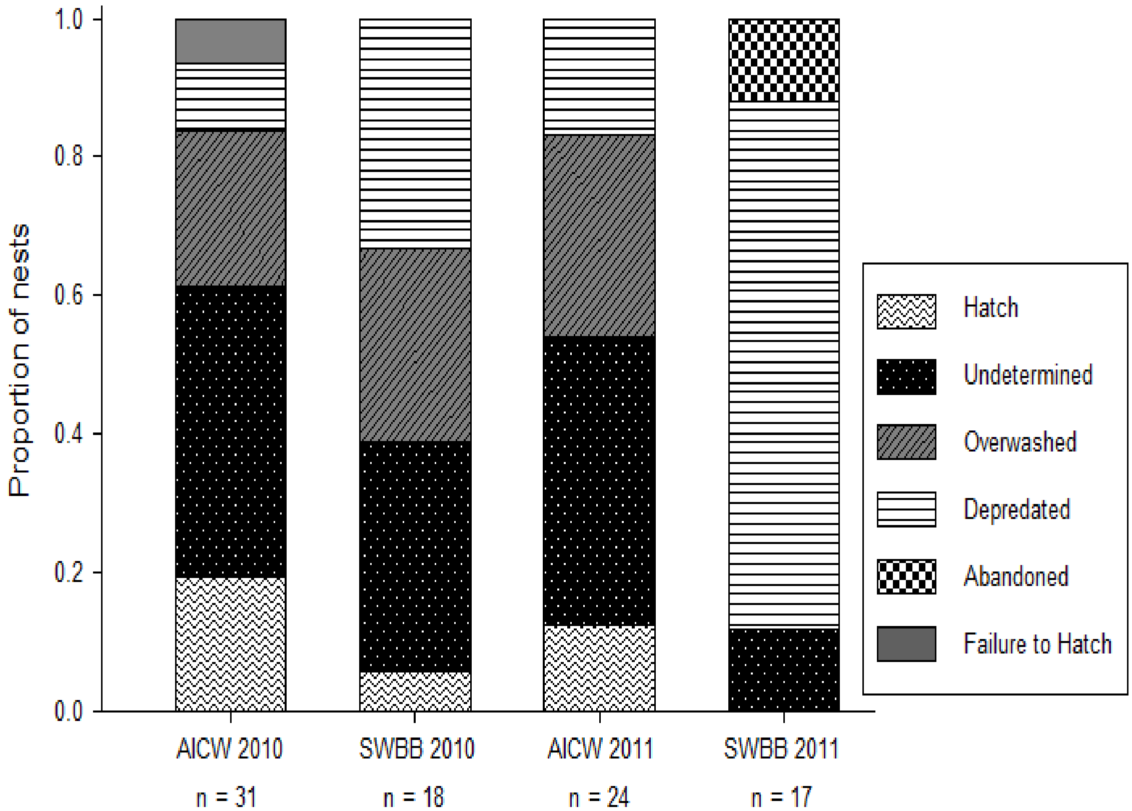

Figure 2.4. Fate of control nests of American Oystercatchers along the Atlantic Intracoastal Waterway (AICW) and southwest Bulls Bay (SWBB), Cape Romain Region, South Carolina, April – July, 2010 and 2011. n = number of nests monitored.

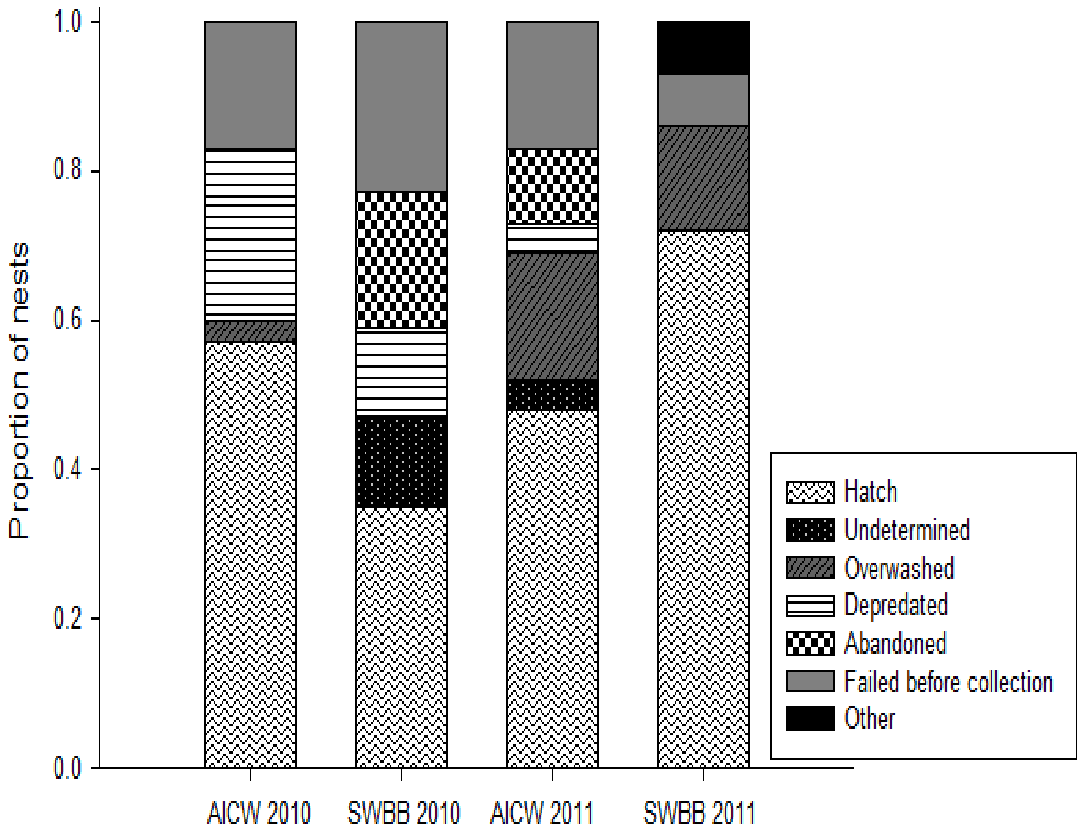

Figure 2.5. Fate of headstart nests of American Oystercatchers along the Atlantic Intracoastal Waterway (AICW) and southwest Bulls Bay (SWBB), Cape Romain Region, South Carolina, April – July, 2010 and 2011.

Table 2.3 Mayfield daily survival rates and probability of hatching success for headstart and control nests of American Oystercatchers in the Cape Romain Region, South Carolina, 2010-2011.

Year	Site	Nest type	No. nests	Exposure days	No. failures	Mayfield daily survival[a]	Probability of success[b]
2010	Atlantic Intracoastal Waterway	Headstart	30	589	13	0.977	0.53
		Control	31	414	25	0.940	0.19
	Southwest Bulls Bay	Headstart	17	305	11	0.966	0.39
		Control	18	190	17	0.911	0.08
2011	Atlantic Intracoastal Waterway	Headstart	23	388	11	0.973	0.48
		Control	24	251	21	0.916	0.09
	Southwest Bulls Bay	Headstart	14	323	3	0.991	0.78
		Control	17	138	17	0.877	0.03
	TOTAL	Headstart	84	1605	38	0.976	0.52
		Control	90	993	80	0.919	0.10

[a] **calculated as # failures/ total exposure days**

[b] **calculated as Mayfield DSR^number of days in the incubation stage (27)**

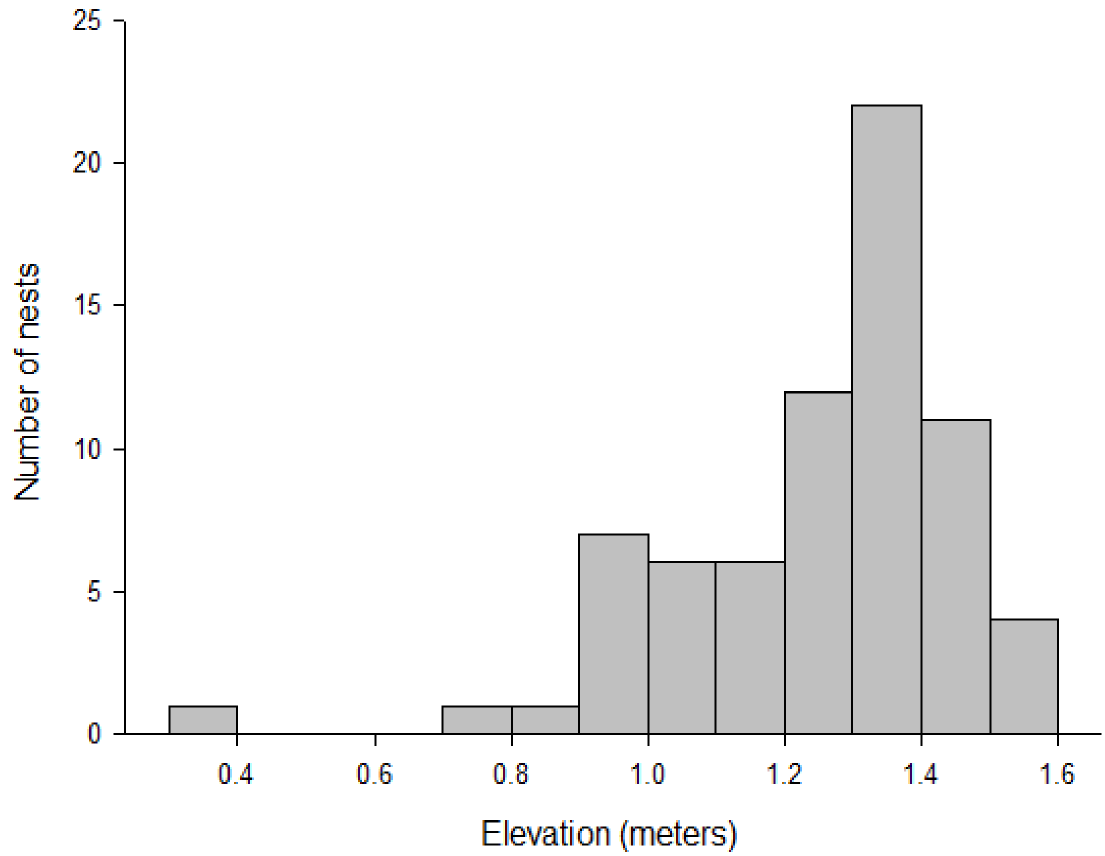

Figure 2.6. Frequency distribution of elevations for American Oystercatcher nesting territories during the 2011 breeding season along the Atlantic Intracoastal Waterway and Southwest Bulls Bay in the Cape Romain Region, South Carolina.

Table 2.4 Mayfield daily survival rates and probability of brood success for headstart and control nests of American Oystercatchers in the Cape Romain Region, South Carolina, 2010-2011.

Year	Site	Nest type	No. nests	Exposure days	No. failures	Mayfield daily survival[a]	Probability of success[b]
2010	Atlantic Intracoastal Waterway	Headstart	17	323	10	0.969	0.33
		Control	6	236	1	0.996	0.86
	Southwest Bulls Bay	Headstart	6	31	6	0.806	0.00
		Control	1	41	0		
2011	Atlantic Intracoastal Waterway	Headstart	11	247	7	0.972	0.37
		Control	13	105	1	0.990	0.72
	Southwest Bulls Bay	Headstart	10	67	9	0.866	0.01
		Control	0	0	0	0	0
	TOTAL	Headstart	44	668	32	0.952	0.18
		Control	20	382	2	0.995	0.83

[a] **calculated as # failures/ total exposure days**

[b] **calculated as Mayfield DSR$^{\wedge\text{number of days in the pre-fledge stage (35)}}$**

Table 2.5 Chick loss by age for headstarted American Oystercatcher chicks in the Cape Romain Region, South Carolina, April – July, 2010 and 2011.

Year	Site	0-6 days	7-13 days	14-20 days	21-27 days	28-34 days	Total
2010	Atlantic Intracoastal Waterway	11	3	0	1	0	15
	Southwest Bulls Bay	5	0	1	0	0	6
2011	Atlantic Intracoastal Waterway	5	1	3	3	0	12
	Southwest Bulls Bay	14	0	0	0	0	14
	TOTAL	35	4	4	4	0	47

CHAPTER III

ATTENDANCE AND BEHAVIOR OF AMERICAN OYSTERCATCHER PARENTS DURING THE BREEDING SEASON IN THE CAPE ROMAIN REGION OF SOUTH CAROLINA

INTRODUCTION

The American Oystercatcher is listed as a species of high concern by the U.S. Shorebird Conservation Plan (Brown et al. 2001). Estimates of breeding pairs indicate that oystercatcher populations are declining in states south of Virginia (Davis et al. 2001). Threats to productivity include predation, climate change, human disturbance, habitat loss, and overwash. It is unknown whether or not current levels of productivity are sufficient to sustain oystercatcher populations. Therefore, understanding factors that may affect the productivity and survival of nests and chicks are needed to effectively manage this species.

South Carolina supports the second highest number of nesting oystercatcher pairs on the Atlantic coast (Sanders et al. 2008). The Cape Romain Region (CRR) of South Carolina provides nesting habitat for oystercatchers on barrier beaches, estuarine islands, as well as washed shell mounds and supports approximately 60% of breeding pairs in South Carolina (Sanders et al. 2008). The Region also serves as an important site for the population during the non-breeding season with *ca*.1900 wintering oystercatchers (Sanders et al 2004). Although the CRR supports high numbers of oystercatchers, wintering estimates provide evidence that these numbers are a small proportion of the total number that once existed in the area (Sanders et al. 2004).

Nest success in many avian species can be strongly related to behavior patterns and attendance rates of breeding adults that subsequently may be related to environmental variables or habitat conditions (Bukacinska et al. 1996; Paredes et al. 2005; Smith et al. 2007). For example, studies on the European Oystercatcher (*Haematopus ostralegus*) have shown that breeding pairs that feed adjacent to their nests and hence have higher rates of attendance also have higher levels of productivity compared to pairs that must leave their nesting territory and commute to foraging grounds (Ens et al. 1992). In American Oystercatchers, optimal territories for nesting individuals appear to be those where parents can simultaneously attend and be vigilant (Nol 1989).

For the American Oystercatcher, males and females cooperate in parental duties and care for chicks until well after fledging. Biparental care can improve incubation efficiency, nest and brood survival, as well as enhancing conditions of the breeding pair to optimize care toward eggs and chicks (Lenington 1980; Oring 1982; Miller 1984; Szekely and Reynolds 1995). Biparental care may be particularly advantageous when predation rates are high. Biparental care would then allow parents to better defend nests or chicks and would also help to ensure that adults have a mate available for re-nest attempts should nest failure occur (Reynolds and Szekely 1997). Breeding pairs that are unable to cooperate efficiently throughout the breeding season may exhibit lower reproductive success and may experience increased energetic demands (Heany and Monaghan 1996; Martin and Ghalambor 1998; Thomas and Szekely 2005; Alrashidi et al. 2010). Successful partners appear to be those that are better able to coordinate contributions to incubation and chick rearing (Nol 1985; Morris 1987). Parental care tactics (such as provisioning) may be shaped by nest predation as well (Martin et al. 2000).

Site selection may influence attendance rates and behavior patterns of adults during the breeding season. For example, closer proximity to food may result in more frequent nest changes because off duty (i.e. non-incubating) parents can relieve on duty parents earlier (Blanken and Nol 1998). This could be advantageous to allow adults to replenish energy stores that can be directed toward nest or chick care. Ens et al. (1992)

found that pairs of European Oystercatchers with the same nesting and feeding territory fledged more young compared to those with separate nesting and feeding territories. In addition, habitat visibility may influence the nature of parental attendance (Blanken and Nol 1998, Hazlitt et al. 2002).

The purpose of this study was to assess parental behaviors and attendance rates that may influence nesting success of American Oystercatchers in a core portion of their breeding range. I measured attendance rates and classified behavior of parents during incubation and chick-rearing at nesting territories during low-tide foraging periods. I then assessed the relationship between a suite of environmental and ecological variables and parental attendance and behavior. Because this research was conducted as part of a larger project to determine the feasibility of using artificial incubation to enhance productivity of American Oystercatchers, I included variables associated with that experiment (i.e., whether or not parents were brooding artificial or original eggs; see Chapter 2) in this study. Attendance rates of Oystercatchers can influence nest success and lifetime reproductive success since eggs and young chicks left unattended become vulnerable to predators and heat or cold stress (Burger and Gochfeld 1991; Schneider and McWilliams 2007). Similarly, behavioral allocation during incubation and chick-rearing may influence nest or brood success or may be influenced by variables such as the nest or chick age, site or year. Understanding behavioral traits and attendance rates during the breeding season may help managers understand why some nesting locations and pairs are more successful than others.

METHODS

Study Area

Nest searches were conducted to locate nesting territories and pairs with active nests during the 2010 and 2011 breeding season in the Cape Romain Region of South Carolina (see Chapter 2). Two study areas were involved in this study; the Atlantic Intracoastal Waterway (AICW) and Southwest Bulls Bay. These areas are critical for research since the majority of American Oystercatcher breeding pairs in South Carolina nest on shell mounds within the Cape Romain Region of the state (Sanders et al. 2008). Shell rakes along the AICW, from marker 67 to 97, and all shell rakes in the southwest section of Bulls Bay (Venning Creek to Bulls Island Creek) were searched every visit until a nest was found. Active nests in Southwest Bulls Bay and along the AICW were checked until chicks fledged or nests failed.

Field Procedures

I attempted to conduct attendance and behavioral surveys for every active nest in Southwest Bulls Bay and along the AICW. I attempted to conduct one survey for each active nest during incubation and another survey for each nest during the chick rearing phase. However, it was common for nests to fail or chicks to be lost before I was able to conduct a survey. All surveys were conducted during low tide (2 hours before to 2 hours after peak low tide) and were 53-90 minutes in duration. I attempted to conduct chick-rearing surveys when chicks were less than one week old, although this was not always possible. Surveys were conducted from land or boat from a distance of at least 150 m so as to minimize potential impacts to behavior (Burger and Gochfeld 1991; Verboven et al. 2001; McGowan and Simons 2006; Sabine et al. 2008).

The attendance rates of both parents on nesting territories (i.e., the area that the breeding pairs defend, includes the waters edge of the shell rake) were noted throughout the duration of the survey. I conducted continuous behavioral observations and recorded attendance times of each parent (i.e., times were noted when parents departed or arrived). I also recorded the time of day, age and number of chicks or eggs for each survey. The behavior for each adult and the duration of each behavior while present on the territory also were recorded throughout the survey. I distinguished between nest types (headstart or control, see Chapter 2) in case breeding pairs demonstrated different attendance rates or behaviors with the use of artificial eggs in headstart nests. Location was recorded continuously during the survey unless the individual was no longer visible or had left the nesting territory. The relative locations of adults and young were recorded when they were visible (e.g. water's edge, top of shell rake). However, this information was not used in any analyses for this study.

Eighteen behaviors were identified and activities were condensed into categories following Sabine et al. (2008) for all incubation and chick-rearing surveys: reproductive (i.e., copulating, incubating eggs, maintaining nest, brooding, and provisioning chick), self-maintenance (i.e., preening, bathing, stretching, hopping, and shaking), locomotion (i.e., flying and walking), forage (i.e., using bill to open prey or probe substrate for prey and drink), rest (i.e., standing or sitting with head turned back and bill tucked under wing), vigilance (i.e., standing with no bill tuck), alarm (i.e., piping display, head bobbing, chasing, being chased, or other agnostic behavior) and unknown.

Statistical Analysis

I used general linear regression (PROC GLM, SAS Version 9.3, SAS Institute Inc., Cary, NC, USA) to examine the percentage of time breeding adults were present at their territory during the low-tide foraging period and the percentage of time during which parents engaged in each behavior while attending. The proportion of total time attended in relation to total time available and the proportion of time exhibited in behavioral categories in relation to total time in attendance were dependent variables in these analyses. I combined the amount of time each parent was present at the nesting territory during the observation period to derive a measure of total attendance for the breeding pair. For example, if parent 1 was on the territory for 50 min of a 60 min observation period, and parent 2 was on the territory for 40 min of the same 60 min observation period, then the percent time attended = ((50 + 40)/120)) = 0.75. Percentages were transformed using the arc sine root transformation to standardize the variance for analyses, although untransformed values are presented throughout for ease of interpretation. I used a manual backward-elimination process for all dependent variables (both incubation and chick rearing) and deleted terms with $P > 0.05$ at each step.

Behavior data for third and fourth attempt nests during incubation were small and unbalanced among site, nest type and nesting attempt number and therefore excluded from subsequent analyses (Table 3.1). Independent variables for backwards elimination models run for attendance and each behavioral category included nest type, site, year, nest age, clutch size and nesting attempt number. Date was not included because it may be confounded with attempt number. Two-way interaction terms included in the incubation models were site * year and site * attempt. I assessed the relationship between nest success (hatch ≥ 1 egg for control nests, hatch or return ≥ 1 chick for headstart nests) and attendance and each behavioral category separately for headstart and control nests using general linear regression models (PROC GLM, SAS Version 9.3, SAS Institute Inc., Cary, NC, USA) with nest success as the dependent variable. I also conducted a correlation analyses (PROC CORR, SAS Version 9.3, SAS Institute Inc., Cary, NC, USA) for first and second attempt nests during incubation for both sites and years to investigate the relationship among behavior variables.

Sample sizes for chick-rearing were small and unbalanced among site, nest type, brood size and attempt number (Table 3.1). Therefore, analyses were limited to a few comparisons, specifically comparisons of attendance and behavior for first and second attempts along the AICW. I pooled data among brood size because there was no significant relationship between attendance and brood size in first attempt headstart or control nests along the AICW ($F_{1,5} \leq 0.09$, $P \geq 0.78$ for each). I then conducted two analyses. First, I assessed the relationship between attendance and year, nest type (headstart or control), brood success (fledge ≥ 1 chick or failed), brood size (1-3), chick age (d), chick age^2 and a two-way interaction term, brood success * year. The variable, chick age^2 was included to allow for a nonlinear relationship between chick age and the dependent variable. Second, I sought a relationship between attendance and year, nesting attempt number (1 or 2), brood success (fledge ≥ 1 chick or failed), brood size (1-3), chick age (d), chick age^2 and a two-way interaction term, brood success * year. Therefore, the difference in the two models was the inclusion or exclusion of the term for nest type (model 1) and attempt number (model 2). Analyses on chick-rearing only included surveys conducted along the AlCW because of limited surveys conducted during this stage in Bulls Bay due to low survival of chicks within this study area. I ran correlation analyses (PROC CORR, SAS Version 9.3, SAS Institute Inc., Cary, NC, USA) separately for first attempt nests during chick-rearing (headstart and control combined), as well as first and second attempt headstart nests along the AICW to investigate how the dependent variables were related to each other.

RESULTS

Incubation

Incubation surveys (n = 52 headstart nests, 26 control nests) were conducted from 10 April – 3 July 2010 and 29 April – 11 June 2011 on first (n=46 surveys) and second attempt nests (n=32 surveys). Eighty-seven nests failed before incubation surveys could be conducted.

Combined attendance of both parents on the nesting territory during low-tide periods ranged from 39% to 100% along the AICW and 57% to 98% in Southwest Bulls Bay for all nests during the 2010 and 2011 breeding season (Figure 3.1). The mean attendance for all breeding pairs for both sites and years was 81.0% ± 14.3% (Table 3.2). The percentage of time breeding pairs spent in reproductive behavior ranged from ca. 40 – 50% for all sites and years (Figure 3.2). Self-maintenance, foraging and vigilance each typically accounted for 10 – 20% of the observation period during incubation while locomotion, resting and alarm behaviors each accounted for <10% of the observation period (Figure 3.2). There were slight differences in the time pairs spent in different behaviors for the two study areas. For example, breeding pairs along the AICW allocated more time to vigilance, resting, and self-maintenance behaviors than those in Bulls Bay (Table 3.3, Figure 3.2). There were no significant differences in attendance time ($F_{1,71}$=0.01, P=0.94) or percent of time allocated to each behavior between nest types (Tables 3.3 and 3.4; $F_{1,76} \leq 1.49$, $P \geq 0.23$ for each). Clutch size was positively related to alarm behaviors observed on nesting territories ($F_{1,76}$=5.46, P=0.02). For first and second attempt nests (headstart and control), the correlation among all pairwise comparisons of behaviors during incubation was low ($r^2 \leq 0.35$ for all pairwise comparisons). Attendance during incubation was positively related to nest success for all control nests between sites and years for first and second attempt nests ($F_{1,22}$ = 8.16, P = 0.01). Attendance was higher at control nests for breeding pairs that hatched ≥ 1 chick (88.83 ± 10.64%) compared to nests that failed (77.59 ± 11.95%). All other behaviors were not found to be significantly related to nest success ($F_{1,50} \leq 1.16$, $P \geq 0.29$ for each behavior for headstart nests; $F_{1,50} \leq 3.19$, $P \geq 0.09$ for each behavior for control nests).

Chick-rearing

Surveys during the chick-rearing stage (n = 7 from control nests, n = 9 from headstart nests) were conducted 6 May – 7 July 2010 and 12 May – 7 July 2011 for first attempt nests. An additional nine surveys were conducted for second attempt nests (headstart nests only) between 10 June and 7 July 2010 and 8 June – 25 June 2011. Approximately 44% (n = 24) of nests monitored between both breeding seasons that hatched ≥ 1 egg or had ≥ 1 chick returned as a headstart chick failed before a chick-rearing survey could be conducted.

Combined attendance of both parents on the nesting territory during low-tide periods ranged from 62.5% to 100% along the AICW during chick-rearing for first and second attempt nests during the 2010 and 2011 breeding season (Figure 3.3). The mean attendance for all breeding pairs along the AICW for both years was 90.4% ± 10.9%. The percent of time breeding pairs were present on nesting territories along the AICW during chick rearing (90%) appeared higher than attendance rates observed for breeding pairs during incubation along the AICW (82%; Tables 3.2 and 3.5). Vigilance and foraging were the primary behaviors of breeding pairs during chick-rearing surveys on the waterway for both years (Figure 3.4). For chick-rearing from first attempts (all nest types) along the AICW, all pairwise comparisons in all cases were weak ($r^2 \leq 0.25$). For chick-rearing first and second attempt in headstart nests along the AICW, all pairwise comparisons in all cases were weak ($r^2 \leq 0.25$).

There was no significant difference in attendance rates between control and headstart nests during chick-rearing (Table 3.6). Results from models run for first-attempt nests only for each behavior during chick-rearing showed that chick age was significantly related to reproductive and locomotion behaviors (Table 3.7). Breeding pairs spent less time in reproductive and locomotion behaviors on nesting territories as chicks aged, although the relationship with chick age and reproductive behavior was nonlinear (Figure 3.5). The data suggest a clear negative relationship between chick age and reproductive behavior through the first 8 days post hatch, but due to the lack of data in chicks >10 days of age it is difficult to determine if the upward sweep in Figure 3.5 is real or an artifact of the sampling methods. Additional data on older chicks would clarify these data. Year was significantly related to self-maintenance behavior ($F_{1,14} = 8.65$, $P = 0.01$). Brood success, nest type, brood size and the interaction term fledge * year were not significant in any of the models ($F_{1,14} \leq 3.89$, $P \geq 0.07$ for each). In addition, there were no significant relationships between attendance and any of the independent variables I assessed ($F_{1,14} \leq 1.09$, $P \geq 0.31$ for each).

The results in the final models of behaviors for first and second attempt nests during chick-rearing for headstart nests indicated that independent variables including chick age, chick age^2 and the interaction term fledge * year were significantly related to behaviors (Table 3.8). Brood success was positively related to the amount of time breeding pairs spent in alarm behavior ($F_{1,16} = 6.85$, $P = 0.02$). Breeding pairs that fledged ≥ 1 chick spent more time in alarm behavior (4.5 ± 2.3%) compared to pairs that did not fledge any chicks (2 ± 1.8%). Chick age was significantly related to reproductive ($F_{1,16} = 7.32$, $P = 0.02$) and foraging ($F_{1,15} = 4.67$, $P = 0.05$) behaviors. There was a clear negative relationship between reproductive behavior and chick age but there was a non-linear relationship between chick age and foraging behavior (Figure 3.6). The data suggest a positive relationship between chick age and foraging behavior through the first 8 days post hatch, but due to the lack of data in chicks >10 days of age it is difficult to determine if the downward sweep in Figure 3.6 is real or an artifact of the sampling methods. Additional data on older chicks would clarify these data. There was also a significant relationship in the final model between foraging behavior and the interaction term brood success * year ($F_{1,14} = 5.39$, $P = 0.04$). Year, nest attempt and brood size were not significantly related to any of the behaviors ($F_{1,16} \leq 1.66$, $P \geq 0.22$). In addition, there were no significant relationships between attendance and any of the independent variables I assessed ($F \leq 0.21$, $P \geq 0.65$).

DISCUSSION

Parental attendance and behavior patterns can be used as a tool to inform management decisions particularly if these data can be related to environmental variables such as habitat type or reproductive variables such as nest or brood success. American Oystercatchers typically have a hatch success of ~40% and brood success of ~20% (Davis et al. 2001; Sabine et al. 2006; Thibault 2008). Within the CRR, the rates of nest success can vary within and between nesting areas and years and it has been suggested that some of that variability may be attributed to attendance (Thibault 2008; Thibault et al. 2010).

I found no effect of nest type (i.e., whether or not parents were assigned to headstart or control nests) on parental attendance or any of the behaviors I recorded during incubation or chick-rearing. These findings were significant because a major part of this study (Chapter 1) involved assessing the feasibility of headstarting. While the first chapter reports the hatching and nest success of assigned headstart compared to control nests along the AICW and in Southwest Bulls Bay, this chapter provides evidence that parents do not alter attendance rates or behavior based on the use of artificial eggs or after the release of headstarted chicks when compared to control nests (i.e., those with original eggs and naturally hatched chicks). These results further indicate that it is possible to headstart eggs without disturbing the reproductive cycle, behavior or attendance rates that are typical during incubation and chick-rearing for American Oystercatcher breeding pairs.

Active nests of ground nesting species such as oystercatchers typically have at least one parent in attendance to reduce losses due to weather or predation (Morris 1987; Burger and Gochfeld 1991). Research has demonstrated that predation and starvation can be major contributors to nest failure in oystercatchers in the southeastern U.S. (Nol 1985; Davis et al. 2001; Sabine et al. 2006). However, while parental attendance of nests decreases the probability of an egg or chick being lost (Verboven et al. 2001), attendance at the nest site also can reduce the amount of food provisioned as the two behaviors are often traded-off. I found that the majority (99%) of surveys conducted during the incubation and chick-rearing stage had at least one adult present on the nesting territory for the duration of the survey. Because predation appears to be common at oystercatcher nests in the CRR (Thibault 2008; also see Chapter 2 herein), behaviors during incubation or chick rearing may be related to the vulnerability of the nest (Thompson and Raveling 1987; Martin et al. 2000). Selection should favor nesting strategies and behaviors that minimize the risk of predation (Smith et al. 2007).

The Skutch hypothesis predicts that nest predation increases with parental activity at the nest and that activity is positively related with clutch size (Skutch 1949). In contrast, other studies investigating parental attendance during incubation have found that nests with lower attendance rates tend to suffer higher rates of egg loss (Thompson and Raveling 1987; Samelius and Alisauskas 2001; Verboven et al. 2001; Smith et al. 2007).

Egg hardiness (ability to tolerate extensive heating and cooling) of oystercatcher eggs could enable reduced parental activity at the nest site (Nol and Humphrey 1994; McGowan and Simons 2006). In this study, clutch size only appeared to be positively related to the amount of time adults spent in alarm behaviors and in particular attendance was not related to clutch size. Nest success of American Oystercatcher nests within the Cape Romain Region does not appear to be negatively influenced by increased activity of breeding pairs on the nesting territory as the Skutch hypothesis predicts but rather enhanced by increased attendance rates of breeding pairs as other studies have found. However, during my study all surveys were conducted during the daytime when mammalian predation may be less prevalent and when parents may be less likely to leave nests unattended due to heat stress. Further investigation on attendance rates of oystercatchers at night would be useful to determine if breeding pairs make adjustments to attendance rates when predation pressure is expected to be greatest and when eggs can be left unattended without risk of damage from heat.

Environmental variables may influence parental behavior during incubation and as such may help explain why nest success may vary among sites and years. Oystercatcher breeding pairs typically coordinate contributions to incubation so that one adult is always incubating the nest (Nol 1985). Because reproductive behavior (i.e., as I classified behaviors) during the nesting stage primarily includes incubation, I found little difference in time allocated to reproductive behaviors between sites and years. All breeding pairs allocated more time spent to self-maintenance, vigilance and rest behaviors, however, along the AICW compared to Southwest Bulls Bay. Smith et al. (2007) found that behavior can be influenced by visibility on nesting locations. Optimal territories for oystercatchers appear to be those where parents can forage and be vigilant simultaneously (Nol 1989). Parents not present on territories are presumably away foraging or at “loafing” sites (Burger and Gochfeld 1991). Bulls Bay may provide nesting habitat of a slightly higher quality compared to the AICW with respect to proximity to food resources. For example, Thibault et al. 2010 found that the extent of shellfish reefs (i.e. foraging areas) adjacent to nest sites was greater in Bulls Bay compared to AICW. It appears, therefore, that if breeding pairs in Bulls Bay foraged on nearby reefs they may have had less time to allocate towards comfort behaviors, such as self-maintenance or rest, compared to pairs on the waterway. Unknown activities appeared to be recorded more frequently for Southwest Bulls Bay and this may have been due to vegetation there obscuring observation of adults.

Research has indicated that predation does not increase with parental activity between nesting stages (Roper and Goldstein 1997; Martin et al. 2000). In this study, attendance of breeding pairs during chick-rearing was not found to be significantly related to the brood success. However, because of limited sample sizes, the potential effect of study site during the chick-rearing stage could not be assessed. A previous study within the CRR by Thibault et al. (2010) found that Southwest Bulls Bay had higher rates of parental attendance for successful broods compared to failed broods while parental attendance along the AICW was higher for failed broods compared to successful broods. Lower occurrences of nest failure caused by overwash and predation were thought to contribute to reproductive success for this area (Thibault 2008). Comparing attendance rates and brood success between the 2010 and 2011 breeding seasons I found that breeding pairs attended nesting territories more during the 2011 season but had decreased brood success. Additional surveys within this area would need to be conducted during the chick-rearing stage within these sites to determine whether or not there is a relationship between attendance and brood success.

Foraging efficiency in breeding oystercatchers may depend at least in part on the distance between foraging locations and the nest (Smith et al. 2007; Thibault et al. 2010). Increased provisioning efforts to larger broods may alter foraging distance, as well as changes in the type and size of prey delivered (Wright et al. 1998; Thibault 2008). To feed chicks, one parent must be off territory while the other parent typically attends to young (Nol 1985). During my study, brood size was not significantly related to attendance or any of the behaviors I measured, including foraging (i.e., time allocated to foraging on or adjacent to the nesting territory). The lack of significance between brood size and attendance or behaviors suggests that oystercatchers at these two study sites can provision broods of various sizes without altering attendance or behavior patterns. Chick age was significantly related to reproductive behavior (negative relationship), locomotion behavior (negative relationship), and foraging behavior (positive relationship). Research has found that cooperation by parents is most important during the first week post hatch when energy requirements for chick growth and survival are maximal (Miller 1984; Byrkjedal 1985; Roberts and Hatch 1993; Blanken and Nol 1998; Thibault 2008) but that the requirements for parents to provision chicks often decrease as the chicks age. Because reproductive behavior includes provisioning the chick and because locomotion may occur more as adults are transferring food from the shoreline to chicks, it is not unexpected that behaviors directly related to feeding chicks (locomotion and reproductive) would be negatively related to chick age as I observed. In contrast, there appeared to be a positive relationship between foraging and chick age for headstart pairs with first and second attempt nests during chick-rearing. Parents foraging on nesting territories may not necessarily be foraging strictly to provision chicks but rather to replenish energy stores. Further study of parental behaviors during chick-rearing, particularly as chicks age and approach fledging, would be beneficial to determine if differences in behavior occur between the two study areas and if these might be due to differences in habitat structure or proximity to food resources. However, this may not be possible if chick loss occurs early on and is related to extrinsic factors such as predation or overwash rather than parental behavior and attendance. As the breeding season progresses, brood attendance may decline as there is more of an energetic risk of survival to adults if they extend brood care too long (Rutherauff et al. 2009). However, I found no significant relationship between the nesting attempt number and attendance or any other behavior during incubation or chick-rearing. It may be useful to further investigate the effect of nesting attempts on attendance and behavior in third and fourth nesting attempts that would likely occur later in the breeding season. While there is documentation of attendance rates changing as the breeding season progresses, little research has been conducted investigating behavioral changes of breeding pairs as the season progresses.

I did not investigate sexual differences in parental care for pairs between the two study areas during these years but it is important to consider findings from other studies to explain individual differences in parental care. The incidence and extent of incubation and brood care can vary between individuals (McKinney and Brewer 1989; Heany and Monaghan 1996; Fraser et al. 2002). Sexual differences in investment often take on different forms and can occur at different times during the breeding season (Morris 1987). For example, both sexes may attend equally during incubation but unequal attendance rates may still occur during chick rearing (Nol 1985, Wiggins and Morris 1986). In American Oystercatchers, Nol (1985) found that females tended to brood more while males made more foraging trips during chick-rearing. I did not differentiate between males from females during my surveys but future analyses that included documenting sexual roles may provide managers with additional data that could explain some of the variability observed in reproductive success among sites and years.

Because the CRR supports the majority of breeding pairs of American Oystercatchers in South Carolina (Sanders et al. 2008), understanding the relationship between environmental variables, parental behaviors, and nest and brood success in this area is important for management. Such data can be used to further understand what, if any, management actions can be taken to improve productivity. My data demonstrated that headstarting may enhance nest success (see Chapter 2) and that parental behavior and attendance is not altered with the use of artificial eggs. Parental behavior may, however, be adjusted in response to other variables such as site characteristics, nesting stage or year. As such, management of American Oystercatchers should consider not just direct causes of reproductive failure but also variability in behavioral attributes of parents during all phases of the breeding season. Additional research that measures parental and chick behavior during brood rearing for different nesting attempts between the two sites (AICW and Bulls Bay) would enhance our understanding of the trade-off between provisioning, foraging and vigilance.

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Table 3.1. Sample sizes of attendance and behavioral surveys conducted for American Oystercatcher control and headstart nests during incubation and chick-rearing for first through fourth nesting attempts along the Atlantic Intracoastal Waterway and Southwest Bulls Bay, Cape Romain Region, South Carolina, 10 April – 7 July 2010 and 29 April – 7 July 2011.

	Southwest Bulls Bay				Atlantic Intracoastal Waterway			
	Attempt 1	Attempt 2	Attempt 3	Attempt 4	Attempt 1	Attempt 2	Attempt 3	Attempt 4
Incubation (Control)	3	5	2*	0	13	5	5*	1*
Incubation (Headstart)	12	8	0	0	18	14	1*	0
Chick-rearing (Control)	1*	0	0	0	7	0	1*	1*
Chick-rearing (Headstart)	2*	0	0	0	9	9	0	0

*** Indicates surveys that were excluded from analyses**

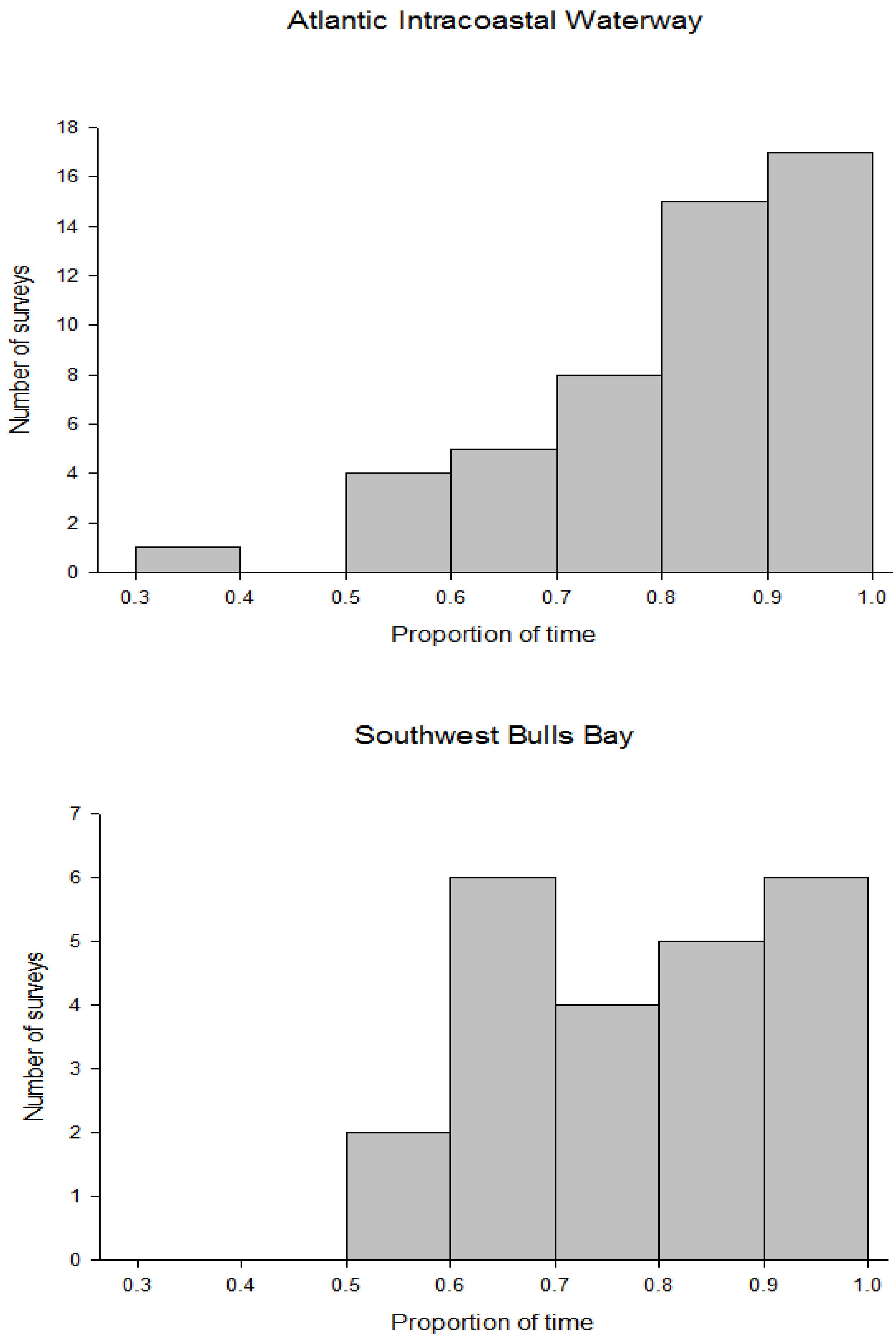


Figure 3.1. Frequency distribution of attendance rates for American Oystercatcher parents nesting along the Atlantic Intracoastal Waterway (top) and Southwest Bulls Bay (bottom) during incubation surveys for first and second attempt nests in the Cape Romain Region, South Carolina, 2010 and 2011 breeding season.

Table 3.2. Attendance rates of American Oystercatcher pairs during the incubation stage for first and second attempt nests in each study area within the Cape Romain Region of South Carolina during the 2010 and 2011 breeding season.

Year	Site	No. surveys conducted	Total survey time (min)	Time present on territory (%)
2010	Atlantic Intracoastal Waterway	32	4050	3336 (82)
	Southwest Bulls Bay	13	1750	1350 (77)
2011	Atlantic Intracoastal Waterway	18	2194	1811 (83)
	Southwest Bulls Bay	10	1390	1091 (78)
TOTAL	Atlantic Intracoastal Waterway	50	6244	5147 (82)
	Southwest Bulls Bay	23	3140	2441 (78)

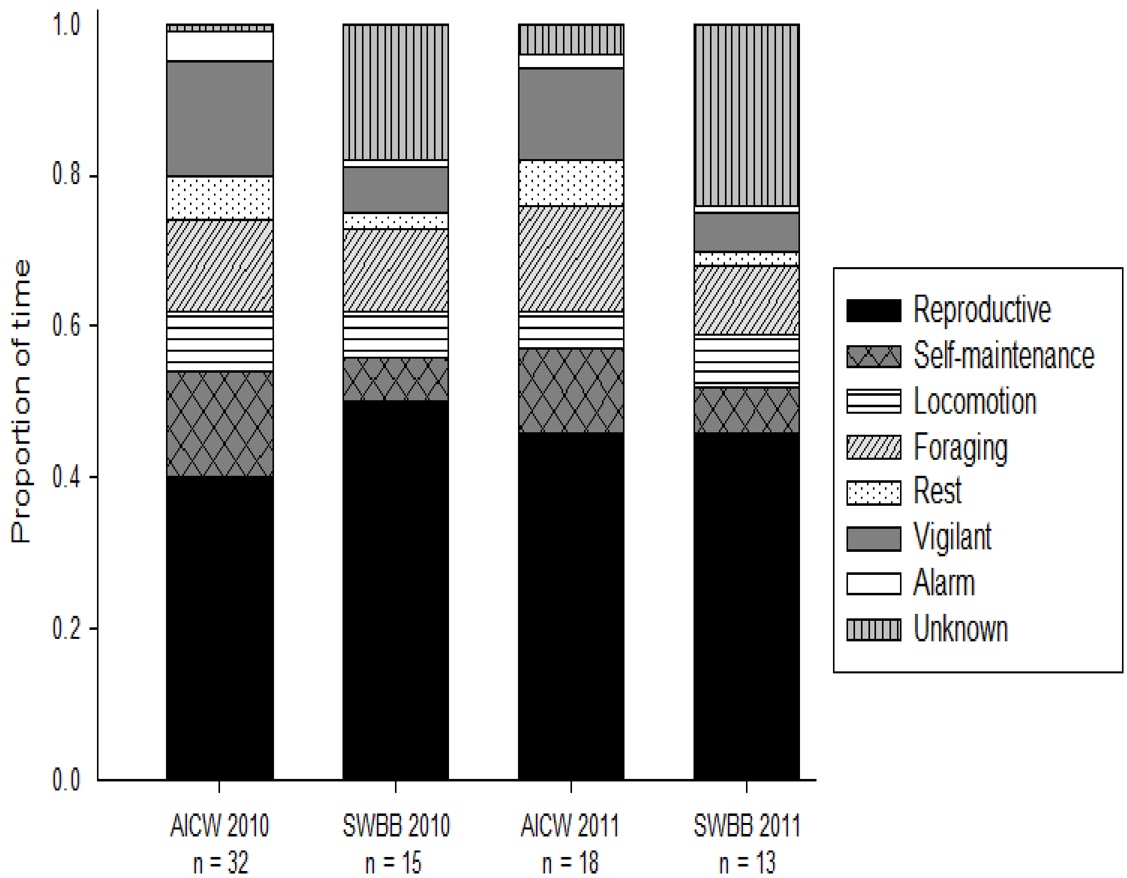


Figure 3.2. Behaviors of American Oystercatcher breeding pairs while attending nesting territories during incubation for first and second attempt nests within the Cape Romain Region, South Carolina, 10 April – 7 July 2010 and 29 April – 7 July 2011. n = number of nests monitored.

Table 3.3. Stepwise results from a backwards elimination procedure to assess the effects of various factors on parental attendance and behaviors of American Oystercatchers during incubation for nests within the Cape Romain Region, South Carolina, USA, 2010 and 2011. Models conducted separately for attendance and for each behavioral category. Number refers to order in which variables were removed from each behavior model during the backwards elimination (P>0.05). F statistic and P-values presented for any significant variables remaining in final model.

	Attendance	Reproductive	Self-maintenance	Locomotion	Foraging	Rest	Vigilance	Alarm
Nest type	4	3	7	3	7	4	5	4
Site	8	8	$F_{1,76}$=7.65 *P*=0.01	5	3	$F_{1,76}$=9.80 *P*=0.003	$F_{1,76}$=13.85 *P*=0.0004	7
Year	6	4	4	6	5	5	6	6
Nest age	3	5	6	4	4	6	4	3
Nesting attempt	7	6	5	8	6	7	3	2
Clutch size	5	7	3	7	8	3	7	$F_{1,76}$=5.46 *P*=0.02
Site * attempt	2	1	1	1	1	2	2	1
Site * year	1	2	2	2	2	1	1	5

Table 3.4. Percent time (mean ± SD) attending and engaged in specific behaviors during incubation for American Oystercatcher pairs during first and second nest attempts within the Cape Romain Region, South Carolina, 2010-2011.

Behavior	Headstart nests (%)	Control nests (%)
Attendance	80.86 ± 15.19	81.54 ± 12.80
Reproductive	46.71 ± 21.20	43.62 ± 21.65
Self-maintenance	10.71 ± 11.93	12.77 ± 10.21
Locomotion	6.35 ± 4.14	7.15 ± 5.56
Foraging	12.17 ± 11.37	10.46 ± 9.93
Rest	4.21 ± 7.07	4.80 ± 6.75
Vigilance	11.10 ± 11.52	11.80 ± 9.30
Alarm	2.29 ± 4.39	2.77 ± 4.34
Unknown	6.50 ± 15.79	6.84 ± 15.01

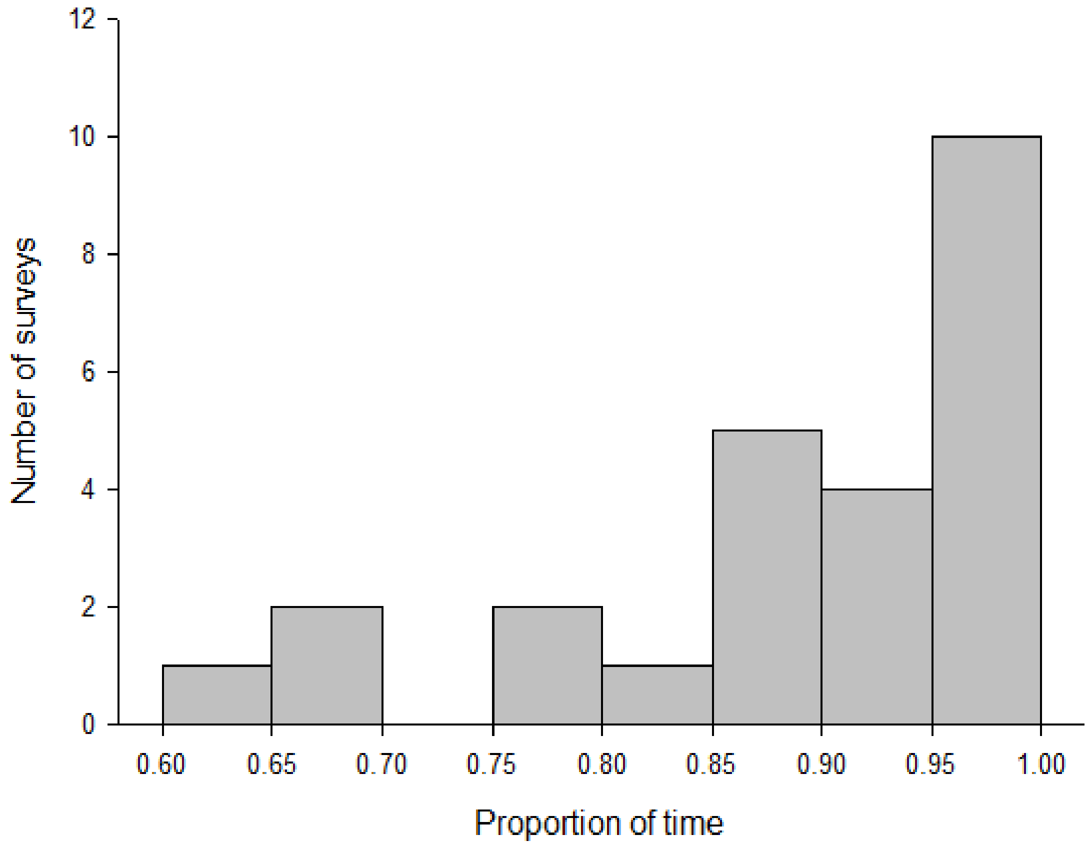


Figure 3.3. Frequency distribution of attendance rates for American Oystercatcher parents nesting along the Atlantic Intracoastal Waterway during chick-rearing surveys for first and second attempt nests in the Cape Romain Region, South Carolina, 2010 and 2011 breeding season.

Table 3.5. Attendance rates of American Oystercatcher pairs during the chick-rearing stage along the Atlantic Intracoastal Waterway within the Cape Romain Region of South Carolina, 2010 and 2011.

Year	No. surveys conducted	Total survey time	Time present on territory (%)
2010	15	1940	1723 (89)
2011	10	1186	1096 (92)
TOTAL	25	3126	2819 (90)

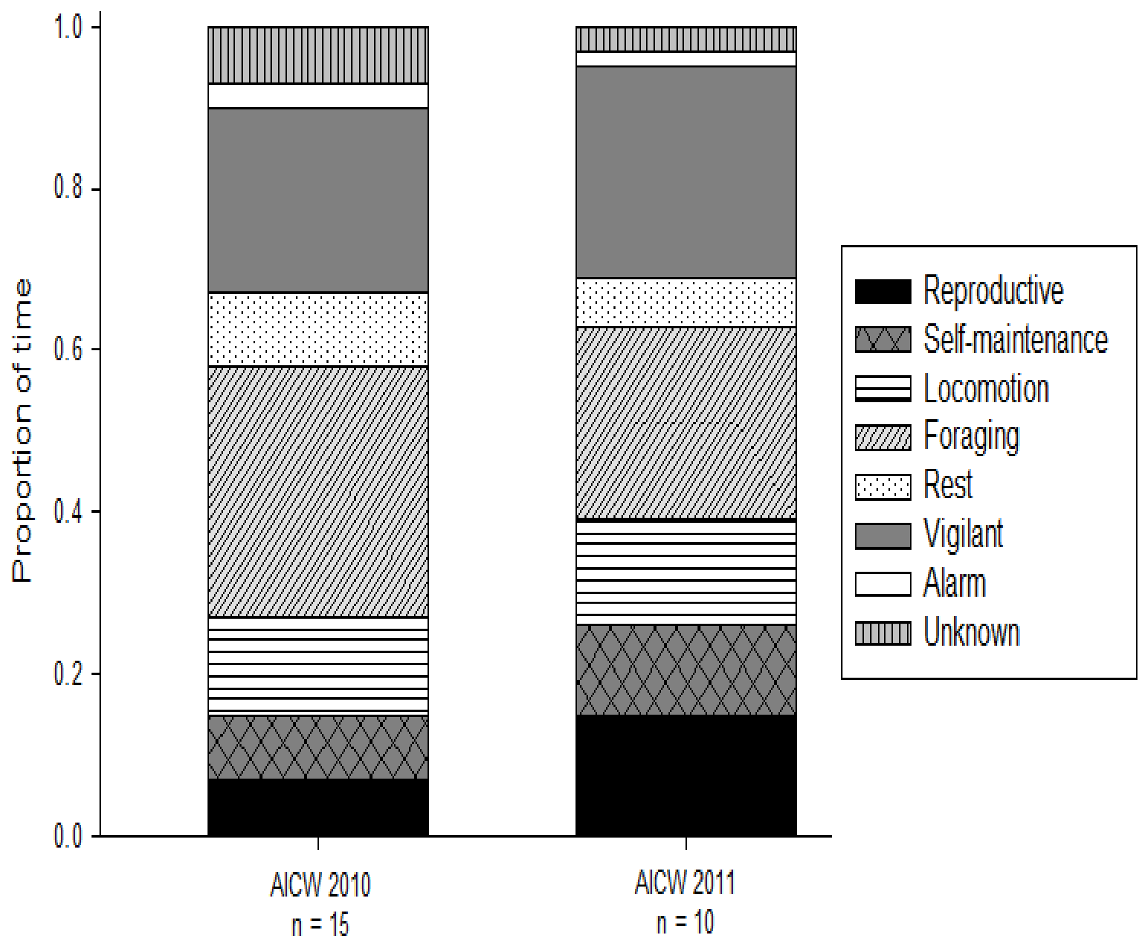


Figure 3.4. Behaviors of American Oystercatcher breeding pairs while attending nesting territories during incubation for first and second attempt nests within the Cape Romain Region, South Carolina, 10 April – 7 July 2010 and 29 April – 7 July 2011. n = number of nests monitored.

Table 3.6. Percent time (mean ± SD) attending and engaged in specific behaviors during incubation for American Oystercatcher pairs during first and second nest attempts within the Cape Romain Region, South Carolina, 2010-2011.

Behavior	Headstart nests (%)	Control nests (%)
Attendance	87.28 ± 13.69	91.57 ± 7.57
Reproductive	15.11 ± 15.5	9.29 ± 8.69
Self-maintenance	9.89 ± 4.40	5.71 ± 1.50
Locomotion	9 ± 6.46	15 ± 14.14
Foraging	25.78 ± 13.37	26.86 ± 23.31
Rest	9 ± 6.69	10 ± 16.13
Vigilance	27.22 ± 22.03	20.14 ± 11.39
Alarm	3.11 ± 3.02	2.43 ± 1.99
Unknown	0.89 ± 1.69	11 ± 23.59

Table 3.7. Stepwise results from a backwards elimination procedure to assess the effects of various factors on parental attendance and behaviors of American Oystercatchers during chick-rearing for first attempt nests within the Cape Romain Region, South Carolina, USA, 2010 and 2011. Models conducted separately for attendance and for each behavioral category. Number refers to order in which variables were removed from each behavior model during the backwards elimination (P>0.05). F statistic and P-values presented for any significant variables remaining in final model.

	Attendance	Reproductive	Self-maintenance	Locomotion	Foraging	Rest	Vigilance	Alarm
Brood success	3	4	2	3	7	3	7	5
Year	7	2	$F_{1,14}$=8.65 *P*=0.01	4	4	4	4	2
Nest type	5	3	4	6	3	5	3	4
Brood size	4	5	3	5	2	2	2	7
Chick age	6	$F_{1,13}$=7.60 *P*=0.01	6	$F_{1,14}$=4.90 *P*=0.04	6	7	6	6
Chick age^2	2	$F_{1,13}$=6.94 *P*=0.02	5	2	5	6	5	3
Brood success * year	1	1	1	1	1	1	1	1

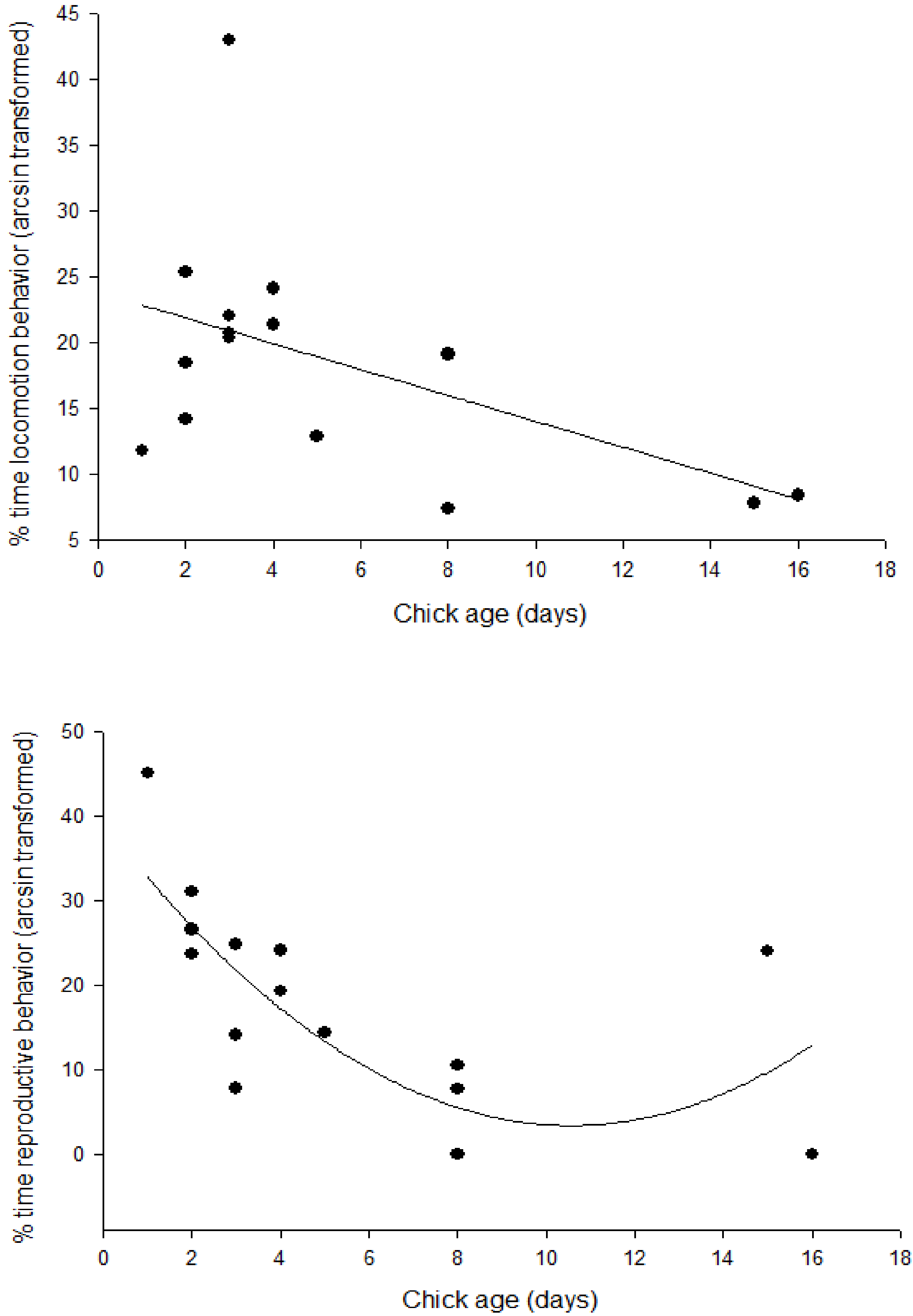
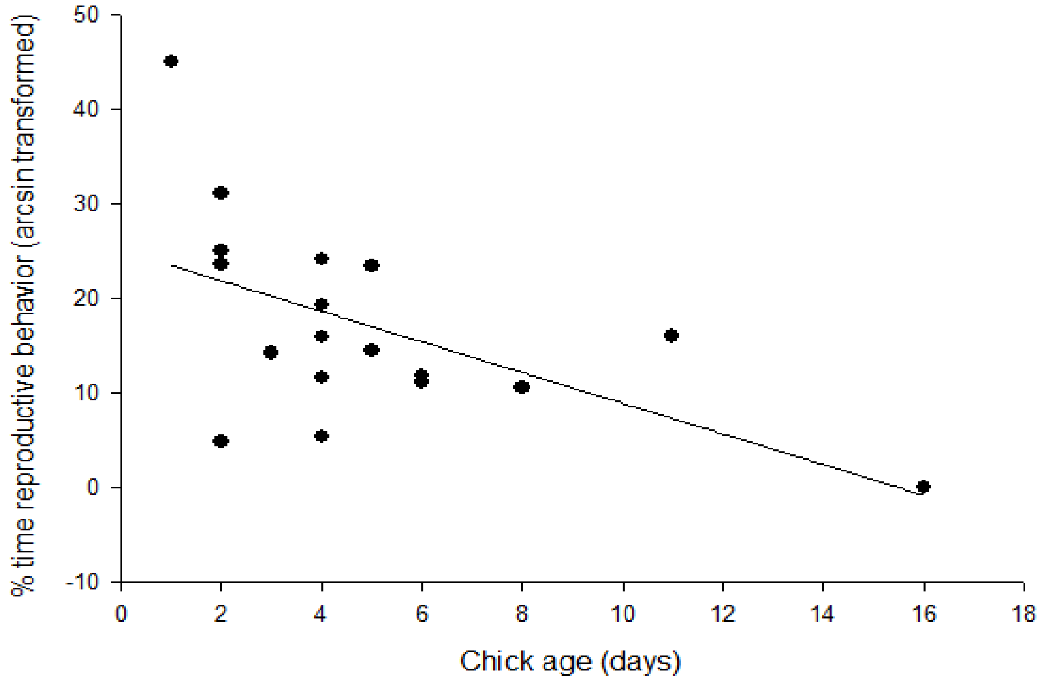


Figure 3.5. Relationship of chick age and locomotion (top) and chick age and reproductive behavior (bottom) during chick-rearing for first- attempt American Oystercatcher nests along the Atlantic Intracoastal Waterway in the Cape Romain Region, South Carolina, 2010 and 2011

Table 3.8. Stepwise results from a backwards elimination procedure to assess the effects of various factors on parental attendance and behaviors of American Oystercatchers during chick-rearing for first and second attempt headstart nests within the Cape Romain Region, South Carolina, USA, 2010 and 2011. Models conducted separately for attendance and for each behavioral category. Number refers to order in which variables were removed from each behavior model during the backwards elimination (P>0.05). F statistic and P-values presented for any significant variables remaining in final model.

	Attendance	Reproductive	Self-maintenance	Locomotion	Foraging	Rest	Vigilance	Alarm
Brood success	3	2	5	$F_{1,14}$=2.16 *P*=0.16	3	6	7	$F_{1,16}$=6.85 *P*=0.02
Year	2	5	7	$F_{1,14}$=0.39 *P*=0.54	5	2	4	2
Nest attempt	4	6	6	2	2	5	6	3
Brood size	7	4	2	1	4	7	5	4
Chick age	6	$F_{1,16}$=7.32 *P*=0.02	4	4	$F_{1,15}$=4.67 *P*=0.05	4	2	5
Chick age^2	5	3	3	3	$F_{1,15}$=5.22 *P*=0.04	3	3	6
Brood success * year	1	1	1	$F_{1,14}$=5.39 *P*=0.04	1	1	1	1



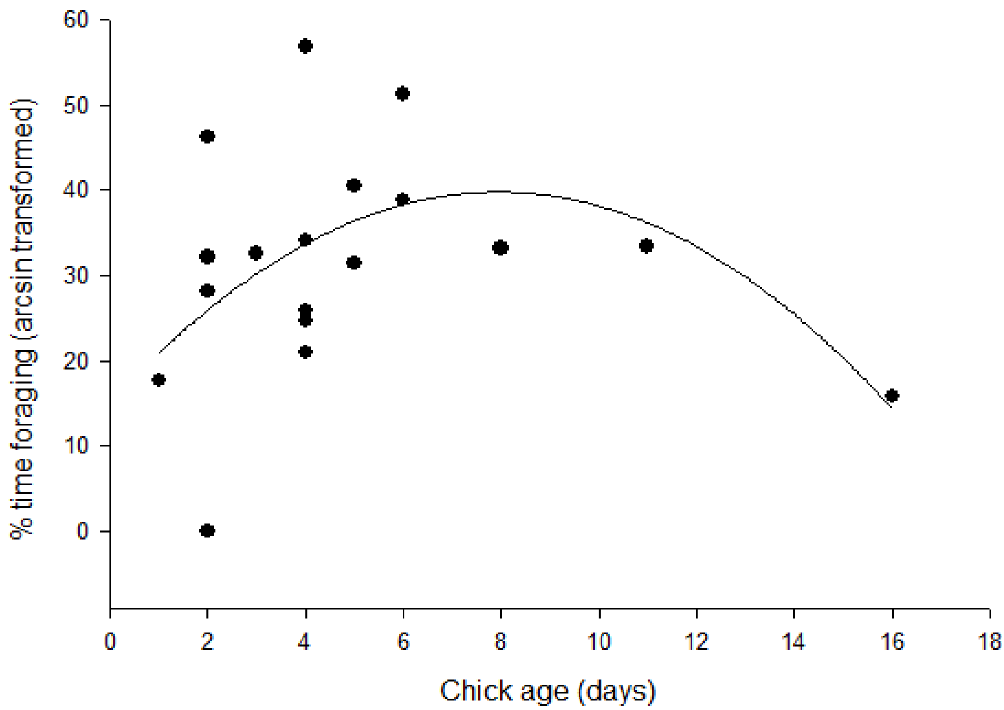


Figure 3.6. Relationship of chick age and reproductive behavior (top) and chick age and foraging (bottom) during chick-rearing for first and second attempt headstart nests of American Oystercatcher nests along the Atlantic Intracoastal Waterway in the Cape Romain Region, South Carolina, 2010 and 2011.

CHAPTER IV

CONCLUSION

American Oystercatchers are long-lived shorebirds with variable annual rates of reproductive success. Coastal development and disturbance due to humans as well as predation of nests and overwash of nest sites are threats to this species during the breeding season. I assessed the feasibility of using a headstarting technique to enhance reproductive success of American Oystercatchers in a core portion of their breeding range in South Carolina. I also investigated attendance and behavioral allocation of breeding pairs on nesting territories during the incubation and chick-rearing stage.

The second chapter of this thesis “Feasibility of Headstarting as a Conservation Tool for American Oystercatchers Within the Cape Romain Region of South Carolina,” investigated the success of headstarted nests compared to control nests in two study areas within the Cape Romain Region, as well as the hatch success and parental acceptance of eggs and chicks artificially incubated. Apparent nest success was higher for headstarted nests compared to control nests but brood success was lower for headstart compared to control nests despite high rates of parental acceptance of headstarted chicks. Although incubator hatch success differed by year, these differences appeared to be due to mechanical issues and settings with the incubator. The acceptance rate for newly hatched chicks by parents was high regardless of whether chicks were placed in their original nest or a foster nest. My data suggest that while headstarting improved nest success, relatively low survival rates of chicks may still contribute to poor reproductive success.

Chapter three, “Attendance and Behavior of American Oystercatcher Parents During the Breeding Season in the Cape Romain Region of South Carolina”, examined the proportion of time that parent oystercatchers were present on the nesting territory and the proportion of behaviors exhibited during the low tide foraging period. Attendance and behavior rates did not vary between assigned headstart and control pairs suggesting that the placement of artificial eggs or headstarted chicks at nests did not adversely affect parental behavior. Parental attendance had a significant positive relationship with nest success during incubation but was not related to brood success. Behaviors of breeding pairs varied by site during incubation and chick age during chick-rearing. Additional chick-rearing surveys should be conducted between sites to assess any potential differences in parental behavior or attendance rates between the two sites during this breeding stage.

Oystercatchers nesting in South Carolina appear to experience high nest loss within the Cape Romain Region. Results from this study indicate that it is possible to headstart nests because a) eggs hatch successfully from the incubator; b) adults continue to incubate artificial eggs; c) parents accept released headstart chicks after hatch; and d) parental behaviors do not change between nest types. Therefore, headstarting can be an effective conservation tool for overcoming productivity loss during incubation. However, high rates of chick loss, as measured in my study, can reduce the usefulness of headstarting. My results demonstrate that wildlife managers need a detailed understanding of both nest and chick survival before deciding whether or not to implement a headstarting program for American Oystercatchers.